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Neogene crabs from Brunei, Sabah and Sarawak

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Synopsis. Thirty-six species of fossil crab are described and figured from the Neogene of Sabah, Sarawak and Brunei. The following 3 genera, 31 species and 3 subspecies are new: *Dorippe frascone tuberculata, Calappa sexaspinosa, Podophthalmus fusiformis, Charybdis feriata bruneiensis, Portunus obvallatus, P. woodwardi, Galene stipata, Parthenope (Rhinolambrus) sublitoralis, Ampliura* (gen. nov.) *simplex, Drachiella guinotae, Iphiculus granulatus, I. miriensis, I. sexspinosus, Leucosia longiangulata, L. serenei, L. tutongensis, Myra brevisulcata, M. subcarinata, M. trispinosa, Nucia borneoensis, N. calculoides, N. coxi, Nucilobus* (gen. nov.) *symmetricus, Pariphiculus gselli beetsi, P. papillosus, P. verrucosus, Philyra granulosa, Typilobus marginatus, Palaeograpsus bittneri, Pinnixa aequipunctata, P. omega, Prepaeduma* (gen. nov.) *decapoda, Xenophthalmus subitus, Macrophthalmus (Mareotis) wilfordi*.

INTRODUCTION

Most of the material forming the basis of the present descriptions was collected by the Geological Survey Departments of Brunei, Sarawak and Sabah (formerly British Territories in Borneo) during the 1950s, and sent to the British Museum (Natural History) in 1958 and 1963–64. A small quantity of material was subsequently supplied by the Brunei Shell Petroleum Company Ltd. The material is only of broad stratigraphical value because of its uniqueness in the fossil record. Reliance was placed on the published ages for the beds by foraminiferal and molluscan workers (Nuttall 1961, Haile & Wong 1965).

A general description of the geology of Sarawak, Brunei and the western part of North Borneo was published by Liechti (1960). Locality S.4918 (see p. 4), originally surveyed by the Geological Survey as Miri Formation (Pliocene) age, was later re-assessed as being of ?late middle Pleistocene age (Wilford 1961). It is probable that locality S.5545 (=S.4965) is of similar age, containing as it does *Charybdis*, an in-shore genus with a modern aspect. The Pleistocene horizons were deposited in valleys which were cut into older strata and later flooded. The Pleistocene horizons represent shallower water than the Mio-Pliocene. Barnes (1968: 337) comments: '*Macrophthalmus* is today littoral, essentially sub-tropical and tropical frequently brackish or estuarine'; there is no reason to suppose that the fossils from Brunei came from a different sort of environment.

A few leucosiids were earlier collected by members of the Geological Survey of North Borneo from isolated areas in the north-east of Borneo; they are clearly from the older Miocene deposits but their stratigraphical control is poor.

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THE FAUNA AND ITS PALAEOECOLOGY

The successive Mio-Pliocene crab faunas from north-west Borneo are unusual, in that they contain an abnormally high proportion of leucosiids (species and specimens) compared with the average of the Indo-West Pacific faunas. Table 1 compares the fossil faunas with data for the Indo-West Pacific region as a whole (taken from Serène 1968: 2804 species in 462 genera) at the present day, and for the nearest comparable Recent fauna, that of the Gulf of Thailand (Rathbun 1910: 207 species in 104 genera). The Gulf of Thailand was chosen because it most closely compares with the quiet waters of Borneo and also has a higher proportion of leucosiids than the normal shelf. The Gulf of Thailand fauna was largely taken by dredge from between the coast and the off-shore fringing islands, an area protected from the high energies of the open shelf with depths ranging from shoreline to about 50 m. The bottom is largely composed of sand and broken shell. Leucosiids generally live in such areas in relatively shallow water. They are weak, sluggish back-burrowers, lurking half-buried for passing prey. It is therefore suggested that the Mio-Pliocene horizons of Borneo were deposited in similar shallow (5–50 m), low-energy areas. The lithology of the rock confirms that the bottom was of sand and broken shell, particularly suited to the back-burrowing leucosiids.

Table 1 Distribution, by percentages in family of superfamily, of crabs from the Recent of the Indo-West Pacific (n = 2804 species in 462 genera; Serène 1968), the Neogene of Borneo (n = 36 species in 22 genera; herein) and the Recent of the Gulf of Thailand (n = 204 species in 107 genera; Rathbun 1910).

	Indo-West Pacific	Borneo (Neogene)	Thailand
Dromiacea	3.4	–	3.0
Raninoidea	0.7	3.0	–
Dorippoidea	1.6	3.0	1.0
Calappidae	1.3	3.0	3.0
Leucosiidae	10.0	65.0	16.0
Majoidea	27.7	3.0	16.0
Portunoidea	7.8	9.0	10.0
Xanthoidea	22.5	3.0	22.0
Hexapodidae	4.7	3.0	13.0
Pinnotheridae	4.3	9.0	5.0
Ocypodoidea	7.3	–	6.0
Grapsoidea	11.7	3.0	10.0

In addition, there are present in Borneo more commensal species of crabs than would be expected, since many are soft-shelled and consequently easily damaged or destroyed before burial. Although there is no direct fossil evidence, annelids and holothurians probably also thrived, which would account for the presence of a higher than average proportion of species (and specimens) of crabs commensal with these animals. The tube-like enrollment of the fossil commensal crabs suggests that sideways walking was already well established.

These suggested conditions invite comparison with the crab fauna collected from the Gulf of Siam (Thailand) by the Danish Expedition to Siam (1899–1900) and described by Rathbun, 1910. She (1910: 303) notes the position of the Gulf of Siam midway between the Indian Ocean and the West Pacific Ocean, and goes on to comment on the high number of new genera and species. This suggested an area particularly suited to speciation, a comment which might be equally true for the crabs of the Pliocene of Borneo. She further noted the abundance of small forms, especially Goneplacidae (*s.l.*) and Leucosiidae, which also show the same dominance in Borneo. Initially Rathbun attributed this bias to 'the zeal of the collector' but later came to realise that it was because the collection was taken from a sheltered arm of the sea. Rathbun recorded 204 species (of which 55 are inshore/estuarine species) in her report, compared with the 36 fossil species (2 inshore/estuarine) in the Borneo fauna here reported.

Some crab groups are clearly underrepresented in the Borneo fauna, particularly the Xanthoidea and Majoidea, but in the Gulf of Siam these are either associated with a very inshore position or found in close association with algae that appear to be absent in Borneo. Serène & Soh (1976), reporting on the Brachyura collected during the Thai-Danish Expedition (1966) from approximately the same area as Rathbun's material, commented particularly on the small size of the specimens. The great majority did not exceed 10 mm. This is also true of many of the species from Borneo, so it is not considered that the Borneo faunas contain a preponderance of juvenile forms.

The two genera *Macrophthalmus* and *Charybdis* from the Pleistocene of Borneo are found in many sublittoral, estuarine or brackish waters around the Indo-Pacific, the predatory *Charybdis* being the more fully marine.

The environment during the Pliocene remained relatively steady. One species (out of 29) survived from the Lower Miri to the Seria and 10 species survived from the Lower Miri to the Upper Miri; one species that appeared in the Upper Miri survived into the Seria Formation. No crabs have been collected from the topmost series of the Borneo Pliocene, the Liang Formation.

STRATIGRAPHY

According to Van Bemmelen (1970), the geosyncline formed on the base-levelled Cretaceous was sinking by the end of the Lower Tertiary, with subsidence continuing into the Upper Tertiary. The basin was being filled by clastic sediments from the central Borneo mountainous spine to the south and from surrounding land masses to the north (Sunda Continent). Umbgrove (1933) called this late cycle geosyncline, in which it lies between stable and mobile areas resulting in weak folding, an ideogeosyncline. Haile (1969) described the formations that make up what he called the North-west Borneo Geosyncline, going on to describe its organization and evolutionary history. He compared and contrasted it with Aubouin's (1965) geosynclinal couple model. Bol & van Hoorn (1980) believed that the parallel ridges were the result of mild compressional movements related to basement wrench faulting. These weak positive areas paralleling the present north-western coastline of Borneo probably acted as barriers to strong wave action, thus having the

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same effect as the fringing islands along the Gulf of Thailand today.

The Miri and Seria Formations of the Belait Group underlie about 647 km^2 of Quaternary in Sarawak and Brunei. Outcrops are mostly to be found in sea cliffs and road cuttings. The Belait Group consists of alternations of clays, sandy clays and sandstones. The main feature-forming beds are the thick sandstone sequences, from which much of the fossil crab fauna has come. The Miri Formation is 1954 m thick at Miri and it can be lithologically and (based on smaller benthonic foraminifera) palaeontologically divided into an upper (1323 m) and a lower (631 m) sequence. The Upper Miri is the more arenaceous, with more rapid but less regular alternations. The Seria Formation (up to 2000 m thick) is conformable with the underlying Miri Formation and is structurally and lithologically similar. It can be separated palaeontologically by the appearance of the foraminifer *Triloculina* 18 (Wilford 1961: 73). The lower beds of the Seria Formation are arenaceous, giving way to sandy and silty clays in the higher beds. The Seria Formation was deposited in a very shallow seaway, with even inshore lagoonal conditions; it was certainly shallower than the preceding Miri Formation sea.

Nearly 4000 m of sediment was deposited during the late Miocene and Pliocene filling of the geosyncline. An unsubstantiated estimate by Schuppli (1946: 4) suggests that during the Neogene of north-west Borneo 50,000 ft (*c*. 15,000 m) of sediment was deposited.

The Liang Formation, which is up to 3000 ft (*c*. 920 m) thick, overlies the Seria Formation, and was deposited on an erosional surface. The Liang is predominantly a marine transgressive series of poorly consolidated sands and clays, changing upwards into similar, but lagoonal or deltaic, sediments. No fossil crabs have been collected from the Liang Formation.

The top boundary of the Liang is an unconformable erosional surface with the overlying Pleistocene terraces. The cause of this was structural, following uplift *en bloc* of the coastal region of north-west Borneo. The denudation was followed by the Jerudong Cycle, which produced a system of mature valleys in which are deposited the Jerudong Terrace sands of ?late Middle Pleistocene age, estuarine or fluviatile in character. This deposit is never more than 10 m in thickness.

LOCALITIES

J.771. Mile 3½ on Labuk Road from Sandakan, Sabah. Undifferentiated Miocene Te_5–f (?Lower Miocene) (Fitch 1958).

NB.130, NB.132. South-east part of Silimpopon region near Tawau, Sabah. Silimpopon horizon of Wenk (1938) which is a clay band lying between the Simengaris Formation and Kapilit Formation, ?Lower Miocene (Te_5–f).

NB.11541. Headwaters of Silabukan River, *c*. 14 km east of Silabukan, Sabah. Segama Group, Tungku Formation, Middle Miocene (upper Tf).

S.4807. Calcareous nodules in sea cliffs at Penanjong, 5 km north-east of Tutong, Brunei. Pliocene, Seria Formation.

S.4918. Base of marine alluvium in road cutting, Mile 3¼ on Muara Road, 8 km north of Brunei Town, Brunei (?late middle Pleistocene – Wilford 1961: 102).

S.4965. See S.5545.

S.5536. Clay ironstone nodules in road cutting Mile 24½ on Tutong Road from Brunei Town, Brunei. Pliocene, Seria Formation.

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S.5538. Mile 19½ on Tutong Road to Brunei Town, Brunei. Pliocene, Upper Miri Formation.

S.5539. Mile 17¾ on Tutong Road to Brunei Town, Brunei. Pliocene, Upper Miri Formation.

S.5544. Mile 13½ on Tutong Road to Brunei Town, Brunei. Pliocene, Lower Miri Formation.

S.5545 (= S.4965). Near Mile 13 on Tutong Road to Brunei Town, Brunei. Late Middle Pleistocene?

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S.5550. Mile 12 on Tutong Road to Brunei Town, Brunei. Pliocene, Lower Miri Formation.

S.10474. Sea cliff *c*. 1.5 km north-east of the mouth of River Trusan, south-west of Miri, Tanjong Batu area, Sarawak. Pliocene, Lower Miri Formation.

S.10475. In sea cliffs. 0.8 km north-east of the mouth of the Batang River, south-west of Miri, Sarawak. Pliocene, Lower Miri Formation but higher in succession than locality S.10474.

SYSTEMATIC PALAEONTOLOGY

Section **PODOTREMATA** Guinot, 1977

Subsection **ARCHAEOBRACHYURA** Guinot, 1977

Superfamily **RANINOIDEA** de Haan, 1841

Family **RANINIDAE** de Haan, 1841

Genus ***RANINOIDES*** H. Milne Edwards, 1837

TYPE SPECIES. By monotypy *Ranina laevis* Latreille, 1825, from the Recent (type locality unknown).

RANGE. Eocene to Recent.

Raninoides sp. Fig. 39

MATERIAL. Two fragmentary external moulds from locality S.5539. Upper Miri Formation: In 61915 (Fig. 39), In 61916.

DESCRIPTION. The full length of neither carapace is preserved, but it probably equalled twice the maximum width which occurs at about midlength; it is moderately rounded to weakly subcarinate in transverse section and longitudinally nearly flat. Gently convex posterolateral margins converge to a posterior margin somewhat narrower than the orbitofrontal margin, which occupies about three-quarters of the width. The very short anterolateral margins terminate at the basal scars of apparently rather small, obliquely-directed spines probably weaker than the flattened outer orbital spine. Posterior to the lateral spine the lateral edges are

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sharply downturned and the sides are inclined almost at right angles.

There is a very small tubercle set immediately behind the lateral spine a little closer to the midline than the margin; it is seen to advantage viewed posteriorly with the carapace held at eye-level. Similarly, a pair of longitudinal nodes are seen close to the midline a little in advance of and between the anterior extremities of short, deep gastrocardiac grooves extending over the median fifth of the carapace length. The cardiac region is weakly defined between the grooves and has a transverse pair of minute tubercles at the widest part.

Discussion. The greater width in proportion to the length of *Raninella toehoepae* Van Straelen 1923, from the Miocene of Borneo, distinguishes that species from *R.* sp.

Section **HETEROTREMATA** Guinot, 1977

Superfamily **DORIPPOIDEA** de Haan, 1833

Family **DORIPPIDAE** de Haan, 1833

Genus ***DORIPPE*** Weber, 1795

Type species. By subsequent designation of Latreille 1810: *Cancer quadridens* Fabricius, 1793 (= *Cancer frascone* Herbst, 1785) [ICZN Opinion 688]; from the Recent of the Indian Ocean.

Range. Miocene to Recent.

Dorippe (Dorippe) frascone (Herbst) ***tuberculata*** subsp. nov. Fig. 1

Diagnosis. Metabranchial regions more nodular than on nominal subspecies. An extra tubercle on either side of midline on the mesogastric region. Anterior part of cardiac region wider (*trans.*), and less prominent node at base of urogastric region. Sternal plates ridged with tubercles and with reduced spines on hepatic regions.

Name. 'Tuberculate'.

Holotype. In 61853 (Figs 1a, b) from the Pliocene, Lower Miri Formation, locality S.5548. Paratypes In 61854–5 from S.5549 and In 61856 from S.5550, Lower Miri Formation.

Description. The carapace is subtrapezoidal in outline, almost flat longitudinally and only slightly arched transversely. The short, slightly convex anterolateral margins are barely interrupted where the cervical furrow reaches the margin; the anterior part of the posterolateral margins is nearly straight, deflected strongly outwards and, in the adult, ending in a sharp spine, but in specimens of approximately one-third the size it continues uninterrupted into the broadly rounded posterior part. A broad ridge bounds the deeply sinuous posterior margin. The orbitofrontal margin is not well preserved; it occupies rather more than half the carapace width. Basal scars indicate strong, obliquely-directed outer orbital spines and somewhat weaker spines at the lower inner orbital angle.

The cervical furrow is wide, fairly deep, and broadly V-shaped to its junction with the hepatic furrows, where it curves back to the margin; the branchiocardiac furrow, issuing from the same notch, is straighter laterally and much more rounded across the midline. Small hepatic regions are depressed and bordered above and below by low ridges, although the anterior ridge is not developed in the younger forms. The protogastric lobes tend to coalesce medially, partially obscuring the anterior process of the small lozenge-shaped mesogastric lobe. There is a low node at the base of each protogastric lobe, a similar one on the mesogastric, one at the base of the epibranchial lobes and another occupies almost all the much reduced mesobranchial lobe. At the base of the crescentic urogastric lobe deep pits, marking the posterior gastric muscles, are bounded by low, oblique ridges. More obvious on the larger specimen is a low, isolated node at the base of the urogastric lobe; the cardiac region has a small median lobe and is more nearly flask-shaped, less rounded than on the smaller carapaces, and acutely V-shaped ridges are more prominently developed. On the metabranchial lobes a weak groove isolates an ovate area on either side of the cardiac region and there is an obscure node anterior to the widest part of the region.

The upper surface of the larger carapace is finely pitted anteriorly, with granules grouped about the nodes; scattered granules on the branchial region become coarser and form rows parallel to the branchial furrows.

The 1st/2nd abdominal sternites are fused with the narrowly triangular, ridged 3rd sternite. The 4th sternites are subtrapezoidal in outline with much attenuated proximal angles leading down between the 5th sternites; near the anterior border a fissure extends half the distance to the midline; a steep ridge rising from the lower lateral angle recurves medially and there is a deep ovate pit on either side of the midline bordering the margin of the 5th sternite. The 5th sternite, scapuloid in outline, is bounded by a low, rounded ridge, while a more distinct median ridge forms the 'spine' terminating in a spinose 'acromion process' overlapping the 4th sternite. The rather more triangular 6th sternite has a convex basal margin and, medially, a well-rounded ridge descends steeply to the lateral margin; its 'acromion process' is formed from a secondary ridge issuing at about 45° from the median one.

Discussion. This subspecies is very close to the nominal subspecies, but differs by having the tubercles along the ridges of the sternal plates. *Dorippe frascone* is distributed widely in the Indo-Pacific from East Africa to Japan and Australia. The nominal subspecies is known to live on sandy-silty or broken shell bottoms at 10–20m depth. None of the fossil specimens shows any sign of an epifauna, which is common on the Recent nominal species.

Superfamily **CALAPPOIDEA** de Haan, 1833

Family **CALAPPIDAE** de Haan, 1833

Genus ***CALAPPA*** Weber, 1795

Type species. By subsequent designation of Latreille, 1810: *Cancer granulatus* Linnaeus, 1758 [ICZN Opinion 712]; from the Recent of the Mediterranean Sea.

Range. Middle? Eocene to Recent.

Calappa sexaspinosa sp. nov. Figs 2a–c

Diagnosis. Carapace with six spines on the flared clypeiform posterolateral margins; the dorsal surface is tuberculate with seven of the tubercles arranged elliptically on the branchial regions.

sharply downturned and the sides are inclined almost at right angles.

There is a very small tubercle set immediately behind the lateral spine a little closer to the midline than the margin; it is seen to advantage viewed posteriorly with the carapace held at eye-level. Similarly, a pair of longitudinal nodes are seen close to the midline a little in advance of and between the anterior extremities of short, deep gastrocardiac grooves extending over the median fifth of the carapace length. The cardiac region is weakly defined between the grooves and has a transverse pair of minute tubercles at the widest part.

DISCUSSION. The greater width in proportion to the length of *Raninella toehoepae* Van Straelen 1923, from the Miocene of Borneo, distinguishes that species from *R.* sp.

Section **HETEROTREMATA** Guinot, 1977

Superfamily **DORIPPOIDEA** de Haan, 1833

Family **DORIPPIDAE** de Haan, 1833

Genus ***DORIPPE*** Weber, 1795

TYPE SPECIES. By subsequent designation of Latreille 1810: *Cancer quadridens* Fabricius, 1793 (= *Cancer frascone* Herbst, 1785) [ICZN Opinion 688]; from the Recent of the Indian Ocean.

RANGE. Miocene to Recent.

Dorippe* (*Dorippe*) *frascone (Herbst) ***tuberculata*** subsp. nov. Fig. 1

DIAGNOSIS. Metabranchial regions more nodular than on nominal subspecies. An extra tubercle on either side of midline on the mesogastric region. Anterior part of cardiac region wider (*trans.*), and less prominent node at base of urogastric region. Sternal plates ridged with tubercles and with reduced spines on hepatic regions.

NAME. 'Tuberculate'.

HOLOTYPE. In 61853 (Figs 1a, b) from the Pliocene, Lower Miri Formation, locality S.5548. Paratypes In 61854–5 from S.5549 and In 61856 from S.5550, Lower Miri Formation.

DESCRIPTION. The carapace is subtrapezoidal in outline, almost flat longitudinally and only slightly arched transversely. The short, slightly convex anterolateral margins are barely interrupted where the cervical furrow reaches the margin; the anterior part of the posterolateral margins is nearly straight, deflected strongly outwards and, in the adult, ending in a sharp spine, but in specimens of approximately one-third the size it continues uninterrupted into the broadly rounded posterior part. A broad ridge bounds the deeply sinuous posterior margin. The orbitofrontal margin is not well preserved; it occupies rather more than half the carapace width. Basal scars indicate strong, obliquely-directed outer orbital spines and somewhat weaker spines at the lower inner orbital angle.

The cervical furrow is wide, fairly deep, and broadly V-shaped to its junction with the hepatic furrows, where it curves back to the margin; the branchiocardiac furrow, issuing from the same notch, is straighter laterally and much more rounded across the midline. Small hepatic regions are depressed and bordered above and below by low ridges, although the anterior ridge is not developed in the younger forms. The protogastric lobes tend to coalesce medially, partially obscuring the anterior process of the small lozenge-shaped mesogastric lobe. There is a low node at the base of each protogastric lobe, a similar one on the mesogastric, one at the base of the epibranchial lobes and another occupies almost all the much reduced mesobranchial lobe. At the base of the crescentic urogastric lobe deep pits, marking the posterior gastric muscles, are bounded by low, oblique ridges. More obvious on the larger specimen is a low, isolated node at the base of the urogastric lobe; the cardiac region has a small median lobe and is more nearly flask-shaped, less rounded than on the smaller carapaces, and acutely V-shaped ridges are more prominently developed. On the metabranchial lobes a weak groove isolates an ovate area on either side of the cardiac region and there is an obscure node anterior to the widest part of the region.

The upper surface of the larger carapace is finely pitted anteriorly, with granules grouped about the nodes; scattered granules on the branchial region become coarser and form rows parallel to the branchial furrows.

The 1st/2nd abdominal sternites are fused with the narrowly triangular, ridged 3rd sternite. The 4th sternites are subtrapezoidal in outline with much attenuated proximal angles leading down between the 5th sternites; near the anterior border a fissure extends half the distance to the midline; a steep ridge rising from the lower lateral angle recurves medially and there is a deep ovate pit on either side of the midline bordering the margin of the 5th sternite. The 5th sternite, scapuloid in outline, is bounded by a low, rounded ridge, while a more distinct median ridge forms the 'spine' terminating in a spinose 'acromion process' overlapping the 4th sternite. The rather more triangular 6th sternite has a convex basal margin and, medially, a well-rounded ridge descends steeply to the lateral margin; its 'acromion process' is formed from a secondary ridge issuing at about 45° from the median one.

DISCUSSION. This subspecies is very close to the nominal subspecies, but differs by having the tubercles along the ridges of the sternal plates. *Dorippe frascone* is distributed widely in the Indo-Pacific from East Africa to Japan and Australia. The nominal subspecies is known to live on sandy-silty or broken shell bottoms at 10–20m depth. None of the fossil specimens shows any sign of an epifauna, which is common on the Recent nominal species.

Superfamily **CALAPPOIDEA** de Haan, 1833

Family **CALAPPIDAE** de Haan, 1833

Genus ***CALAPPA*** Weber, 1795

TYPE SPECIES. By subsequent designation of Latreille, 1810: *Cancer granulatus* Linnaeus, 1758 [ICZN Opinion 712]; from the Recent of the Mediterranean Sea.

RANGE. Middle? Eocene to Recent.

Calappa sexaspinosa sp. nov. Figs 2a–c

DIAGNOSIS. Carapace with six spines on the flared clypeiform posterolateral margins; the dorsal surface is tuberculate with seven of the tubercles arranged elliptically on the branchial regions.

NAME. 'Six-spined'.

HOLOTYPE. In 61857 (Figs 2a–c), a small specimen possibly a juvenile. Pliocene, Lower Miri Formation, locality S.5548. Paratypes In 61858–61 from same locality.

OTHER MATERIAL. In 61862 (S.5544), an abraded specimen only possibly assigned to this species.

DESCRIPTION. The carapace is subtrapezoidal with the beaded edge of the anterolateral margin giving way to five broadly triangular spines, increasing in size posteriorly, followed shortly by a smaller spine on the flared posterolateral margin. This flared portion is very thin and is preserved only on the left side of the type. The posterior margin is probably as wide as the front, which occupies about half the carapace width immediately in front of the flare. The broadly triangular front is downturned and constricted just above the apex; it is produced slightly beyond the outer orbital angle. The orbits are subcircular and obliquely inclined; the upper orbital margins are thickened and have two feeble notches.

Broad furrows separate the median gastric and cardiac regions from the branchial regions. On each of the protogastric lobes, which are separated from the front by a shallow transverse depression, are two tubercles, the smaller, median one slightly in advance; anterior to the tubercles is a transverse row of eight granules. There is a large tubercle with a smaller one behind it on the mesogastric lobe; one on the urogastric and two in line on the cardiac region. Of the four tubercles on each hepatic lobe, the larger anterior pair are *en échelon* with the posterior pair. The epibranchial lobe has three tubercles in a transverse line, and the mesobranchial two small ones. On the metabranchial lobes, seven tubercles are arranged more or less elliptically. Two or three granules may be scattered within the enclosed area.

Fine, pitted grooves on the metabranchial lobes extend more or less parallel with the lateral margins.

The sides are directed sharply inwards and the pleural suture and concave buccal margins are bounded by ridges.

DISCUSSION. *Calappa sexaspinosa* is closest to the Recent species *C. lophos* (Herbst, 1782) but *C. sexaspinosa* has a very different distribution of tubercles. It differs from *C. hepatica* (Linnaeus, 1758) by its greater clypeiform extension of the posterolateral margin. *C. pustulosa* Alcock, 1896 is also very similar, but this species has virtually no clypeiform extension, giving a length/breadth ratio of 1:1 as opposed to 0.7:1 for *C. sexaspinosa*.

Superfamily **PORTUNOIDEA** Rafinesque, 1815

Family **PORTUNIDAE** Rafinesque, 1815

Subfamily **PODOPHTHALMINAE** Miers, 1886

Genus ***PODOPHTHALMUS*** Lamarck, 1801

TYPE SPECIES. By monotypy *Podophtalmus* [sic] *spinosus* Lamarck, 1801 [= *Portunus vigil* Fabricius, 1798]; from the Recent of the Indo-Pacific Region.

RANGE. Oligocene to Recent.

Podophthalmus fusiformis sp. nov. Figs 48–53

DIAGNOSIS. Carapace fusiform with straight, transverse upper orbital margins and well-rounded outer orbital angles; the lateral angle is at one third of the distance from the front.

NAME. 'Spindle-shaped'.

HOLOTYPE. In 62066 (Figs 48a, b). Paratypes In 62067 (Fig. 49), In 62068 (Fig. 50), In 62069 (Fig. 53), In 62070 (Fig. 51), In 62071 (Fig. 52), In 62072–96. All water-rolled internal moulds from locality S.5550, Lower Miri Formation.

DESCRIPTION. The carapace is fusiform in outline and about twice as long as broad. The rostrum (as seen on the latex mould) is very narrow, taking up only about a tenth of the orbitofrontal margin; it is steeply downturned and has a shallow median sulcus. Rather deep ocular constrictions lead to gently sinuous, almost straight upper orbital margins. The outer orbital spine was probably very weak and the lower orbital margin extends beyond the upper to the extent of the rostrum. The anterolateral margins, well rounded in front and gently concave behind, lead to strong, probably blunt spines set a little anterior to midlength, and directed slightly backwards. Sinuous posterolateral margins, rather longer than the anterolateral margins, lead by shallow coxigeal incisions to narrowly rounded posterior angles. The posterior margin is slightly convex and about half the width of the front. The cervical furrow curves forwards from immediately in front of the lateral spine, deepening at its junction with the hepatic furrow; it turns steeply backwards and inwards to the outer angle of the mesogastric lobe where it becomes deeper and more steeply inclined; at the base of the lobe it turns almost at right angles and terminates at a narrow incursion of the confluent urocardiac lobe.

The regions are distinct and slightly tumid. The mesogastric lobe is small and pentagonal; its very narrow, parallel-sided anterior process extends to the upper orbital margin and continues as an inconspicuous ridge onto the body of the lobe. A ridge on the lateral spine becomes obsolete as it progresses across the epibranchial lobe and the small, ovate mesobranchial lobes are rather more distinctly separated from the epibranchial than the metabranchial lobes. A weak branchiocardiac furrow follows the downward curve of the epibranchial ridge, reaching the margin anterior to the coxigeal incision. The urogastric and cardiac lobes together are broadly pentagonal and wider than the mesogastric lobe.

Only the male abdomen is preserved; it forms an attenuated triangle extending just into the 4th abdominal sternites; the narrow telson is about one sixth the length of the 6th somite, which is as long as the fused 4th/5th somites. The 3rd sternites are lozenge-shaped, the 4th subrectangular and the 5th–7th are chordate.

DISCUSSION. As preserved *Podophthalmus fusiformis* seems to lack the outer orbital spine of the genus. *P. vigil* (Fabricius) has orbits sloping backwards strongly, causing much reduced anterolateral margins; the lateral spines appear to be shorter than in *P. fusiformis*.

Subfamily **PORTUNINAE** Rafinesque, 1815

Genus ***CHARYBDIS*** de Haan, 1833

TYPE SPECIES. By subsequent designation of Glaessner, 1929: *Cancer sexdentatus* Herbst, 1783 (= *C. feriatus* Linné, 1758) [ICZN Opinion 712]; from Recent of the Indian Ocean.

RANGE. Oligocene to Recent.

NAME. 'Six-spined'.

HOLOTYPE. In 61857 (Figs 2a–c), a small specimen possibly a juvenile. Pliocene, Lower Miri Formation, locality S.5548. Paratypes In 61858–61 from same locality.

OTHER MATERIAL. In 61862 (S.5544), an abraded specimen only possibly assigned to this species.

DESCRIPTION. The carapace is subtrapezoidal with the beaded edge of the anterolateral margin giving way to five broadly triangular spines, increasing in size posteriorly, followed shortly by a smaller spine on the flared posterolateral margin. This flared portion is very thin and is preserved only on the left side of the type. The posterior margin is probably as wide as the front, which occupies about half the carapace width immediately in front of the flare. The broadly triangular front is downturned and constricted just above the apex; it is produced slightly beyond the outer orbital angle. The orbits are subcircular and obliquely inclined; the upper orbital margins are thickened and have two feeble notches.

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DISCUSSION. *Calappa sexaspinosa* is closest to the Recent species *C. lophos* (Herbst, 1782) but *C. sexaspinosa* has a very different distribution of tubercles. It differs from *C. hepatica* (Linnaeus, 1758) by its greater clypeiform extension of the posterolateral margin. *C. pustulosa* Alcock, 1896 is also very similar, but this species has virtually no clypeiform extension, giving a length/breadth ratio of 1:1 as opposed to 0.7:1 for *C. sexaspinosa*.

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RANGE. Oligocene to Recent.

Podophthalmus fusiformis sp. nov. Figs 48–53

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NAME. 'Spindle-shaped'.

HOLOTYPE. In 62066 (Figs 48a, b). Paratypes In 62067 (Fig. 49), In 62068 (Fig. 50), In 62069 (Fig. 53), In 62070 (Fig. 51), In 62071 (Fig. 52), In 62072–96. All water-rolled internal moulds from locality S.5550, Lower Miri Formation.

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Only the male abdomen is preserved; it forms an attenuated triangle extending just into the 4th abdominal sternites; the narrow telson is about one sixth the length of the 6th somite, which is as long as the fused 4th/5th somites. The 3rd sternites are lozenge-shaped, the 4th subrectangular and the 5th–7th are chordate.

DISCUSSION. As preserved *Podophthalmus fusiformis* seems to lack the outer orbital spine of the genus. *P. vigil* (Fabricius) has orbits sloping backwards strongly, causing much reduced anterolateral margins; the lateral spines appear to be shorter than in *P. fusiformis*.

Subfamily **PORTUNINAE** Rafinesque, 1815

Genus ***CHARYBDIS*** de Haan, 1833

TYPE SPECIES. By subsequent designation of Glaessner, 1929: *Cancer sexdentatus* Herbst, 1783 (= *C. feriatus* Linné, 1758) [ICZN Opinion 712]; from Recent of the Indian Ocean.

RANGE. Oligocene to Recent.

Charybdis (Charybdis) feriata (Linné) ***bruneiensis*** subsp. nov. Figs 41, 42

1961 *Charybdis* sp. Ball, *in* Wilford: 102, 152; pl. 39 (*pars*).

DIAGNOSIS. A faint transverse ridge on the cardiac region.

NAME. 'From Brunei.'

HOLOTYPE. A part-decorticated carapace of a male, In 59015 (Figs 41a–c), from locality S.4965. Paratype In 59012 (Fig. 42), from S.4918. Both ?late Middle Pleistocene.

DESCRIPTION. The carapace is broadly ovate, the length being about four fifths of the width measured at the base of the lateral spines. In longitudinal section there is a moderate frontal depression; when viewed from the front the lateral margins are somewhat attenuated and slightly upturned. The orbitofrontal margin is about two thirds of the carapace width; no details of the front, which takes up half this distance, are preserved. Broadly ovate orbits are inclined a little outwards from the midline, and of the two notches in the slightly upturned upper orbital margin the outer is close to the outer orbital spine. Basal scars along the anterolateral margins indicate there were probably six spines. They appear to have been ovate in section, with the third about half the size of the first and succeeding pairs and the sixth thorn-like. Weakly rounded posterolateral margins lead by wide, shallow, slightly raised depressions for the 5th coxae to a broad, rounded posterior margin.

The regions are well defined, the median ones flatly tumid. On each protogastric lobe there is a short transverse ridge, almost uniting at the midline; from this ridge a triangular portion of each protogastric lobe encloses the anterior part of the semicircular mesogastric lobe. A stronger ridge crossing the broadest part of that lobe is similarly interrupted at the midline and immediately in front a low ridge develops into the anterior process which continues to the base of the small, rounded frontal lobe. Posteriorly the mesogastric lobe is divided by a furrow and its outer margins are lined with four or five granules. The urogastric lobe is represented by a small granular ridge. The cardiac region is lingulate in outline; anteriorly it is medially divided and there is a vague ridge; it becomes somewhat scabrous posteriorly. From the lateral spine a thin ridge curves the length of the epibranchial lobe. A broad depression encloses the mesobranchial lobe; between this lobe and the cardiac region is a low, rounded node and together the tumid areas form a semicircle about the mesogastric lobe.

A row of even-sized granules extends behind the upper orbital margin, there are a few atop the mesobranchial lobe and others of several diameters are scattered randomly over the dorsal surface.

On the underside deep marginal notches, giving way to shallow furrows, separate the 3rd from the 4th sternites. Shallower notches separate the 4th from the otherwise fused 5th sternites, the posterior angles of which are extremely drawn out to embrace the margin of the chordate 6th sternites; the 7th/8th are of much the same size and subreniform, while the 9th is much smaller and triangular in outline.

The right cheliped is slightly larger than the left. The anterior border of the merus has three spines of which the proximal one is the smallest. A large blunt process occurs at the inner angle of the carpus which has three spinules on the outer margin. The propodus, with five smooth costae, has two strong ridges with a spine at the distal end of each. There is also a spine on the anterior face near the carpal articulation. The fingers are about the same length as the palm.

DISCUSSION. Our species must be assigned to *Charybdis* (s.str.) because it does not have granular patches behind the epibranchial spine (*Gonioneptunus*), nor the curved posterior border of *Goniohellenus*. There are six anteriolateral teeth on the Brunei specimens, of which five are large; this rules out *Gonioinfradens* which has four large and two small. The Brunei species has only a very faint cardiac ridge; it is therefore unlikely to belong to *Goniosupradens* which has a distinct cardiac ridge. Of the 29 Recent species of *Charybdis (Charybdis)*, 7 fall within the geographic range of *C. bruneiensis: C. affinis* Dana, 1852; *C. annulata* (Fabricius, 1798); *C. feriata* (Linnaeus, 1758); *C. japonica* (Milne Edwards, 1861), *C. lucifera* (Fabricius, 1798), *C. milesi* (de Haan, 1835) and *C. rosaea* (Jacquinot & Lucas, 1853). Of these species *C. japonica, C. annulata* and *C. lucifera* are proportionately broader than *C. bruneiensis*. The other species differ in the spinosity of the chelipeds, except for *C. feriata* which is like *C. bruneiensis* in having four spines on the merus and three on the anterior border of the propodus. Similarly *C. bruneiensis* has the characteristic notched first anterolateral spine as in *C. feriata*. They differ in that *C. bruneiensis* does not have transverse ridges on the anterior part of the mesogastric and protogastric regions, but has a faint transverse ridge on the cardiac.

Genus ***PORTUNUS*** Weber, 1795

TYPE SPECIES. By subsequent designation of Rathbun, 1926: *Cancer pelagicus* Linnaeus, 1758 [ICZN Opinion 394]; from Recent, type locality not known. The International Commission on Zoological Nomenclature in reaching its decision on the type species appears to have overlooked the selection by H. Milne Edwards (July 1840) of *Portunus puber* (Linnaeus, 1767).

RANGE. Miocene to Recent.

Portunus obvallatus sp. nov. Figs 43–45

DIAGNOSIS. Carapace transversely subovate; anterolateral margins with eight spines, with the largest spine at the lateral angle; regions poorly defined and metabranchial region depressed.

NAME. 'Fortified'.

HOLOTYPE. In 61947 (♂, Fig. 43). Paratypes In 61948 (♂, Fig. 44), In 61949 (Fig 45), In 61950–6. All from locality S.5539, Upper Miri Formation. Paratype In 61957 from S.5549, Lower Miri Formation.

DESCRIPTION. A *Portunus* about half as long as broad and broadest at about midlength; moderately convex in longitudinal section, rather more steeply downturned in front and transversely almost flat. The narrowly rounded anterolateral margins have seven more or less evenly-sized granular spines followed by much larger sharp, slightly upturned spines at the lateral angles projecting straight out. The front is not well preserved; it takes up half the orbitofrontal margin, which occupies rather less than half the overall width. As far as can be made out, the outer orbital spine was weak, probably not extending beyond the front; the lower orbital margin extends

Charybdis (Charybdis) feriata (Linné) ***bruneiensis*** subsp. nov. Figs 41, 42

1961 *Charybdis* sp. Ball, *in* Wilford: 102, 152; pl. 39 (*pars*).

DIAGNOSIS. A faint transverse ridge on the cardiac region.

NAME. 'From Brunei.'

HOLOTYPE. A part-decorticated carapace of a male, In 59015 (Figs 41a–c), from locality S.4965. Paratype In 59012 (Fig. 42), from S.4918. Both ?late Middle Pleistocene.

DESCRIPTION. The carapace is broadly ovate, the length being about four fifths of the width measured at the base of the lateral spines. In longitudinal section there is a moderate frontal depression; when viewed from the front the lateral margins are somewhat attenuated and slightly upturned. The orbitofrontal margin is about two thirds of the carapace width; no details of the front, which takes up half this distance, are preserved. Broadly ovate orbits are inclined a little outwards from the midline, and of the two notches in the slightly upturned upper orbital margin the outer is close to the outer orbital spine. Basal scars along the anterolateral margins indicate there were probably six spines. They appear to have been ovate in section, with the third about half the size of the first and succeeding pairs and the sixth thorn-like. Weakly rounded posterolateral margins lead by wide, shallow, slightly raised depressions for the 5th coxae to a broad, rounded posterior margin.

The regions are well defined, the median ones flatly tumid. On each protogastric lobe there is a short transverse ridge, almost uniting at the midline; from this ridge a triangular portion of each protogastric lobe encloses the anterior part of the semicircular mesogastric lobe. A stronger ridge crossing the broadest part of that lobe is similarly interrupted at the midline and immediately in front a low ridge develops into the anterior process which continues to the base of the small, rounded frontal lobe. Posteriorly the mesogastric lobe is divided by a furrow and its outer margins are lined with four or five granules. The urogastric lobe is represented by a small granular ridge. The cardiac region is lingulate in outline; anteriorly it is medially divided and there is a vague ridge; it becomes somewhat scabrous posteriorly. From the lateral spine a thin ridge curves the length of the epibranchial lobe. A broad depression encloses the mesobranchial lobe; between this lobe and the cardiac region is a low, rounded node and together the tumid areas form a semicircle about the mesogastric lobe.

A row of even-sized granules extends behind the upper orbital margin, there are a few atop the mesobranchial lobe and others of several diameters are scattered randomly over the dorsal surface.

On the underside deep marginal notches, giving way to shallow furrows, separate the 3rd from the 4th sternites. Shallower notches separate the 4th from the otherwise fused 5th sternites, the posterior angles of which are extremely drawn out to embrace the margin of the chordate 6th sternites; the 7th/8th are of much the same size and subreniform, while the 9th is much smaller and triangular in outline.

The right cheliped is slightly larger than the left. The anterior border of the merus has three spines of which the proximal one is the smallest. A large blunt process occurs at the inner angle of the carpus which has three spinules on the outer margin. The propodus, with five smooth costae, has two strong ridges with a spine at the distal end of each. There is also a spine on the anterior face near the carpal articulation. The fingers are about the same length as the palm.

DISCUSSION. Our species must be assigned to *Charybdis* (s.str.) because it does not have granular patches behind the epibranchial spine (*Gonioneptunus*), nor the curved posterior border of *Goniohellenus*. There are six anteriolateral teeth on the Brunei specimens, of which five are large; this rules out *Gonioinfradens* which has four large and two small. The Brunei species has only a very faint cardiac ridge; it is therefore unlikely to belong to *Goniosupradens* which has a distinct cardiac ridge. Of the 29 Recent species of *Charybdis (Charybdis)*, 7 fall within the geographic range of *C. bruneiensis: C. affinis* Dana, 1852; *C. annulata* (Fabricius, 1798); *C. feriata* (Linnaeus, 1758); *C. japonica* (Milne Edwards, 1861), *C. lucifera* (Fabricius, 1798), *C. milesi* (de Haan, 1835) and *C. rosaea* (Jacquinot & Lucas, 1853). Of these species *C. japonica, C. annulata* and *C. lucifera* are proportionately broader than *C. bruneiensis*. The other species differ in the spinosity of the chelipeds, except for *C. feriata* which is like *C. bruneiensis* in having four spines on the merus and three on the anterior border of the propodus. Similarly *C. bruneiensis* has the characteristic notched first anterolateral spine as in *C. feriata*. They differ in that *C. bruneiensis* does not have transverse ridges on the anterior part of the mesogastric and protogastric regions, but has a faint transverse ridge on the cardiac.

Genus *PORTUNUS* Weber, 1795

TYPE SPECIES. By subsequent designation of Rathbun, 1926: *Cancer pelagicus* Linnaeus, 1758 [ICZN Opinion 394]; from Recent, type locality not known. The International Commission on Zoological Nomenclature in reaching its decision on the type species appears to have overlooked the selection by H. Milne Edwards (July 1840) of *Portunus puber* (Linnaeus, 1767).

RANGE. Miocene to Recent.

Portunus obvallatus sp. nov. Figs 43–45

DIAGNOSIS. Carapace transversely subovate; anterolateral margins with eight spines, with the largest spine at the lateral angle; regions poorly defined and metabranchial region depressed.

NAME. 'Fortified'.

HOLOTYPE. In 61947 (♂, Fig. 43). Paratypes In 61948 (♂, Fig. 44), In 61949 (Fig 45), In 61950–6. All from locality S.5539, Upper Miri Formation. Paratype In 61957 from S.5549, Lower Miri Formation.

DESCRIPTION. A *Portunus* about half as long as broad and broadest at about midlength; moderately convex in longitudinal section, rather more steeply downturned in front and transversely almost flat. The narrowly rounded anterolateral margins have seven more or less evenly-sized granular spines followed by much larger sharp, slightly upturned spines at the lateral angles projecting straight out. The front is not well preserved; it takes up half the orbitofrontal margin, which occupies rather less than half the overall width. As far as can be made out, the outer orbital spine was weak, probably not extending beyond the front; the lower orbital margin extends

beyond the thinly ridged upper orbital margin. A weak anterior-facing 'ridge' reaches only a short distance along the lateral spine and the epi- and metabranchial lobes are slightly tumid rather than ridged. The cervical furrow is straight where it crosses the midline, then turns sharply forward and becomes obsolete before reaching the margin. There is a short longitudinal groove at the base of the poorly-defined mesogastric lobe and on either side of the groove are one or two granules; the anterior mesogastric process is barely separated from the protogastric lobes. The cardiac region is broadly hexagonal and wider than the mesogastric lobe. On either side of the cardiac region is a low, rounded 'ridge' with a tubercle at its posterior end, and the metabranchial lobe is depressed against this ridge and behind the epigastric lobe.

Discussion. The diminutive marginal spines anterior to the prominent one at the lateral angle distinguish *P. obvallatus* from *Portunus woodwardi* sp. nov. (below); the posterior margins of the latter are angular rather than sinuous as in *P. obvallatus* which also has a less lobate dorsal surface. The arrangement of the lateral spines is not unlike that of *Portunus sanguinolentus* (Herbst, 1769); otherwise there is no obvious comparison with other species figured from Sagami Bay by Sakai (1965) or Hawaii by Edmondson (1954).

Portunus woodwardi sp. nov. Figs 46, 47

Diagnosis. Carapace with eight anterolateral spines, the seventh vestigial and the eighth at the lateral angle; the mesogastric lobe is partially divided medially and its anterior process extends to the base of the frontal lobes.

Name. After Dr H. Woodward, palaeontologist.

Holotype. In 61923 (♂, Figs 46a, b). Paratypes In 61924 (♂, Figs 47a, b), In 61925–36. All from Pliocene, Lower Miri Formation, of locality S.5548. Paratypes In 61937–45 from Upper Miri Formation, S.5539.

Description. The carapace is broader than long, with the anterolateral margins forming a broad semicircle with the front. The broadly ovate orbits take up the outer fourths of the orbitofrontal margin. The front is not well preserved on any of the available specimens. There is a single notch in the upper orbital margin and behind the short, triangular outer orbital spine are six more or less even-sized subquadrate spines followed by a smaller one which is more conspicuous on the internal mould and, for the most part, incorporated by the shell thickness into the much attenuated spine at the lateral angle. The interstices between the spines are deeply U-shaped and alternate pairs are marked by a short groove extending onto the carapace. Short posterolateral margins converge rapidly to moderate excavations for the 5th coxae and the posterior margin is weakly convex.

Low, oblique ridges separate subrectangular protogastric lobes from frontal and epigastric lobes. The hepatic region is separated by a slight furrow from the gastric region, and from the branchial region by a forwardly curved epibranchial ridge extending from the lateral spine to ovate mesobranchial lobes. The uro- and mesogastric lobes form a single, almost pentagonal area and the slender, slightly tapering anterior process reaches the base of the frontal lobes. The cardiac region is pentagonal and somewhat elongated posteriorly; anteriorly it is weakly divided medially by a furrow which extends a short way onto the urogastric lobe. The metabranchial region has two almost confluent nodes close to the epibranchial and cardiac borders, but is depressed laterally. There is a small ovate node tucked between the mesobranchial lobe and cardiac region.

The tumid areas of the dorsal surface are crowded with rather coarse granules which become sparser and smaller posteriorly.

On the underside of the male the 1st–3rd sternites are transversely narrowly triangular; the 4th are trapezoidal and somewhat indented by the abdominal trough; the 5th and 6th are subrectangular, tapering a little medially; the 7th are rather more rectangular, while the 8th are triangular in outline. Numerous granules crowding the surface become finer posteriorly.

One specimen, In 61924 (Figs 47a, b) has on its left side a swelling typically caused by a parasite, *Bopyrus* sp.; its remarkably large size so strongly affected the natural development of the branchiostegal areas, as well as the dorsal region, that all the anterolateral spines became completely atrophied and the lateral angle rounded. This parasite is of uncommon occurrence among fossil portunids.

Discussion. While no precise details of the front of *P. woodwardi* sp. nov. are available for comparison, it is nonetheless close to *Portunus arabicus* (Woodward, 1905) from the ?Pliocene of the Mekran coast, but in the latter the anterior process of the mesogastric lobe terminates at the transverse 'ridge'; the mesogastric lobe of *P. woodwardi* is proportionately larger, less rounded than that of *P. arabicus* and is divided by a median furrow. *P. woodwardi* is also close to *Portunus gladiator* Fabricius, 1798, but in the latter species anterolateral spines are more triangular and the spaces between them V-shaped.

Superfamily **XANTHOIDEA** Dana, 1851

Family **XANTHIDAE** Dana, 1851

Genus ***GALENE*** de Haan, 1833

Type species. By monotypy *Cancer bispinosus* Herbst, 1783 [ICZN Opinion 85]; from Recent of the Indo-Pacific.

Range. Miocene to Recent.

Galene stipata sp. nov. Figs 54, 55

Diagnosis. *Galene* with extraorbital spine and three lateral spines.

Name. 'Guarded'.

Holotype. In 59014 (Figs 54a–d) from the Pliocene, Lower Miri Formation of locality S.4965. Paratypes: In 61958 (Fig. 55), In 61981 from S.5548, In 61971–80 from S.5549, both Lower Miri Formation; In 61961–70 from Pliocene, Upper Miri Formation, S.5538; In 61959–60 from Pliocene, Seria Formation, S.5537.

Description. The anterior mesogastric process is parallel-sided for half its length; thereafter it tapers to a point terminating level with the upper orbital margins. The front follows the carapace curvature and is half the width of the orbitofrontal margin; it has a narrow median notch extending back as a groove on the dorsal surface; the inner pair of lobes are rounded, very close together and extend beyond the outer pair which form the inner orbital spines. The orbits are subovate and the wide upper orbital margin, bounded in part

beyond the thinly ridged upper orbital margin. A weak anterior-facing 'ridge' reaches only a short distance along the lateral spine and the epi- and metabranchial lobes are slightly tumid rather than ridged. The cervical furrow is straight where it crosses the midline, then turns sharply forward and becomes obsolete before reaching the margin. There is a short longitudinal groove at the base of the poorly-defined mesogastric lobe and on either side of the groove are one or two granules; the anterior mesogastric process is barely separated from the protogastric lobes. The cardiac region is broadly hexagonal and wider than the mesogastric lobe. On either side of the cardiac region is a low, rounded 'ridge' with a tubercle at its posterior end, and the metabranchial lobe is depressed against this ridge and behind the epigastric lobe.

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by a fine groove, has a beaded row of granules interrupted by two feeble notches; between the granules and groove there is a row of pits.

Where it crosses the midline, the cervical furrow is acutely V-shaped and very shallow round the base of the mesogastric lobe; from the forward angle of the mesogastric it extends in a moderately deep, broad curve forwards and outwards to the margin. The median part of the furrow becomes obsolete as growth advances and on larger specimens a false impression of its course is given by the stronger, straighter groove between the urogastric and cardiac lobes. Within the cervical furrow the posterior gastric pits are set very close together and, on specimens ranging up to at least 12.0 mm in carapace width, cuneiform pits mark the position of the internal mandible adductor muscles.

Granules of several diameters crowd the dorsal surface, those posterior slightly the larger. Sub-surface shell layers show groups of pits particularly on the more tumid areas except the cardiac region where they are arranged marginally.

The 1st–3rd abdominal somites are fused in both the male and female, the distal margin is straight, medially concave, laterally convex; a depression, broadening posteriorly, deepens from the medial concavity. A notch between the 1st–3rd and 4th sternites leads back at *c.* 65° and gives way to a broadly curved groove. The 4th sternites are rhomboidal, a broad groove runs from the distal notch to a broadly rounded posterolateral angle. The 5th sternites are half the length of the 4th and subrectangular, the 6th are somewhat longer and more quadrate, the 7th are about half the width of the 6th while the 8th are much reduced and triangular. The abdominal trough extends almost to the anterior margin of the 4th sternites. There is a scattering of granules on the 1st–3rd sternites, particularly near the margins, and on the neighbouring parts of the 4th sternites. The male abdomen tapers moderately from the 3rd somites and the telson-apex is broadly rounded. The ovate female abdomen reaches its broadest at the 4th somite; the length of the rounded-triangular telson exceeds that of the 6th somite.

DISCUSSION. Young forms are somewhat flatter in longitudinal section, more distinctly lobate and granulated and at this stage closely resemble *Lobonotus* spp. – particularly in the small node flanking the cardiac region separated from the metabranchial lobe. In *Galene stipata* this node becomes disproportionately larger as growth advances and less sharply separated from the metabranchial lobe. Also, the protogastric lobes of *G. stipata* are entire, with no tendency towards the bilobed development common to *Lobonotus*.

The present species from Brunei is very close to *Galene obscura* Milne Edwards, 1865, in that it has the extraorbital spines, a groove on the metabranchial region and a spine at the posterolateral angle. Their length/width proportions are very similar but Milne Edwards (1865) recorded five spines on the lateral margin of *G. obscura* whilst only three can be determined on *G. stipata*. *Galene stipata* differs from *Galene bispinosa* (Herbst, 1783) in all the characters stated by Milne Edwards for that species.

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TYPE SPECIES. By original designation *Cancer contrarius* Herbst, 1804 from Recent of the East Indies.

Parthenope (Rhinolambrus) sublitoralis sp. nov. Fig. 40

DIAGNOSIS. The carapace is pentagonal, nearly as long as broad, with its margins lined with tubercles increasing in size posteriorly; the branchial regions are ridged and the dorsal surface bilaterally ornamented with unequal-sized granules.

NAME. 'Below the shore'.

HOLOTYPE. In 61917 (Figs 40a, b) from locality S.5548, Lower Miri Formation. Paratypes In 61918–22 the same locality and horizon.

DESCRIPTION. The carapace is broadly pentagonal, almost as long as broad and deeply depressed between the gastric and branchial regions and, in side view, highest at the cardiac region. There are two or three small granules on the very short anterolateral margins. The short anterior part of the posterolateral margin curves broadly with the lateral angle, and the posterior part is nearly straight; the margins are lined with seven or eight granular tubercles gradually increasing in size posteriorly. A thin ridge bounds the gently convex posterior margin and there is a small tubercle at each angle. The orbitofrontal margin is narrow and slightly elevated. As preserved the rostrum appears to have been not much produced, moderately downturned and sulcate.

From an obscure marginal notch the cervical furrow curves broadly to the angle of the mesogastric lobe, turns sharply inwards and terminates in a pit on either side of the midline. The hepatic region is small and depressed with three or four granules. Shallow constrictions separate the protogastric lobe from the small, subovate mesogastric lobe, the anterior process of which continues to the base of the rostrum. On the protogastric lobes are two rows of four granules, the innermost pair the larger; the mesogastric lobe has two large granules each flanked by a small one, and small granules flank a median one on the urogastric lobe. Several granules encircle a larger median one on the cardiac region and the oblique branchial elevations are also ornamented with unequal granules.

Parallel granulated ridges on the subhepatic and pterygostomian regions extend to the lower outer angle of the orbit. A single ridge on the branchiostegite curves in to the lower angle of the buccal margin, which is quadrate, wider than long.

Of the thoracic sternites, the first pair are very small and slightly indented from the 2nd; these are weakly delineated from the 3rd, which are subovate and deeply separated medially; together they form an obtuse triangle bounded by a raised rim. The 4th sternites are quadrate and the 5th–8th rectangular; on each of the latter is a median granule and another occurs on the outer border.

DISCUSSION. The new species is very similar to *Rhinolambrus pelagicus* (Rüppell, 1830) from the Recent of the Red Sea, but has tubercles on the branchial regions in lines separated by deep branchial grooves. Each axial region has a single large tubercle with a varying number of subsidiary tubercles, compared with the more numerous but randomly distributed tubercles on *R. pelagicus*. A Recent species from an unknown locality, *Rhinolambrus contrarius* (Herbst, 1804) has a similar

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distribution of tubercles but differs by having only one groove crossing the branchial region instead of the two in *R. sublitoralis*. All other species of *Rhinolambrus* have branchial processes and are therefore clearly distinct from *R. sublitoralis*. There is some similarity between the new species and *Platylambrus serratus* (H. Milne Edwards, 1834) from the Recent of the 'Indian Ocean' [*recte* west Central America, see Rathbun, 1925: 516], but the latter has the hinder part of the posterolateral margins more concave and there are a greater number of tubercles on the anterior part of the posterolateral margins.

Superfamily **LEUCOSIOIDEA** Samouelle, 1819

Family **LEUCOSIIDAE** Samouelle, 1819

Genus ***AMPLIURA*** nov.

TYPE SPECIES. *Ampliura simplex* gen. et sp. nov. from Pliocene, Seria Formation of Borneo.

DIAGNOSIS. Wide subcircular female abdomen, buccal cavity initially widening forwards; non-spinate, beaded lateral margins. Length to width ratio 0.85 or less. Hepatic furrows vestigial or absent.

NAME. From Latin *amplus*, large + Greek οὐρά, tail. Feminine.

DISCUSSION. Differs from *Typilobus* by its globose female abdomen and beaded lateral margins. *Nucia* also has a globose female abdomen, but differs from *Ampliura* by its spinate lateral margin and normal leucosiid buccal cavity.

In the weak development of furrows, except for the furrows bounding the cardiac region, and absence of lateral spines *Typilobus obscurus* Quayle & Collins, 1981, from the Upper Eocene of southern England, may be an early member of the genus but its abdomen is unknown; it otherwise differs by being almost circular in outline. Another species with scarcely defined regional furrows and smooth lateral margins is *Typilobus modregoi* Via Boada, 1969, but maximum width appears to occur anterior to the middle, unlike most leucosiids which have their greatest width at the middle or just posterior to it. A second species from the same horizon and locality, *Typilobus boscoi* Via Boada, 1969, resembles *Ampliura* with its female abdomen (Gómez-Alba, 1988) and vestigial hepatic grooves, but differs from it in having spinate lateral and posterior margins and normal leucosiid triangular buccal cavity.

Ampliura simplex gen. et sp. nov. Fig. 3

DIAGNOSIS. The carapace is subovate, without lateral spines and only feebly indented at the cervical notch; the cervical and hepatic furrows are inconspicuous.

NAME. 'Simple', from the absence of any marginal processes.

HOLOTYPE. In 62157 (Fig. 3), a female from locality S.5537, Seria Formation.

DESCRIPTION. The carapace is transversely subovate with broadly rounded lateral angles, the length being about three-quarters of the breadth; transversely and longitudinally flattened and with hardly any postfrontal depression. Only the merest indentation at the cervical notch interrupts the broadly rounded anterolateral margins. The orbitofrontal margin occupies about half the carapace width; no details of the front are preserved, but the orbits are very small and circular.

The hepatic and lateral part of the cervical furrows are present as vague lines between the granules; the grooves separating the urogastric and cardiac lobes from one another and from the branchial regions, however, are more clearly defined. The mesogastric lobe is discernible rather by the grouping of granules than by any clear-cut groove. The cardiac is broader than the mesogastric lobe and more or less shield-shaped; it very slightly indents the urogastric in front and probably almost touches the posterior margin behind.

The entire dorsal surface is densely covered in flattened granules of several diameters extending over the rounded lateral edges and sides.

There is a fine groove above the subtriangular pterygostomian region; the outer shell surface near the front is missing: had it been preserved, this part of the region would in all probability have been visible in dorsal view. Oviducts open into fifth sternites.

DISCUSSION. See generic discussion.

Genus ***DRACHIELLA*** Guinot *in* Serène & Soh, 1976

TYPE SPECIES. By original designation *Lithadia sculpta* Haswell, 1880, from the Recent of Fitzroy I., Queensland, Australia.

Drachiella guinotae sp. nov. Fig. 9

DIAGNOSIS. Regional grooves divide the branchial region into its component epi-, meso- and meta- regions. Cardiac region circumscribed by furrows. Protogastric region clearly differentiated. Eyes visible on dorsal surface.

NAME. In honour of Dr Danièle Guinot.

HOLOTYPE. A female carapace, In 61863 (Figs 9a–c) from *c.* 1 mile NE of R. Trusan, SW Miri, Tanjong Batu area, Sarawak; Lower Miri Formation.

DESCRIPTION. Carapace transversely subovate, length almost 0.8 of the width, widest about midlength; steeply rounded transversely and in side view steeply rounded from behind the front to the cardiac region which forms a second prominence. Distinct furrows extend from the posterolateral angles to the front, at which point they are separated by the ridged anterior mesogastric process; lobulate marginal tubercles completely isolated from all the dorsal regions. There is a deep indentation between paired tubercles at the lateral angles and one on the anterolateral margins. The straight posterolateral margins have a tubercle behind the lateral pair and another just before the ridged intestinal lobe. The intestinal lobe overhangs and gives a false impression of the posterior margin from which it is separated by a fine groove. From the anterolateral tubercle a short concave tuberculate ridge leads to the outer angle of the orbit. A thin ridge of four to five granules forms the upper orbital margin barely divided from the narrow, almost straight, bluntly depressed front. A groove leading back from the front separates prominent frontal lobes joined behind by the anterior mesogastric process. The very small circular orbits are directed obliquely upwards and divided by a strong septum from somewhat larger, deeper antennal fossae. The epistome appears to have been narrow and acutely V-shaped.

The cervical furrow is obtuse and very shallow where it

distribution of tubercles but differs by having only one groove crossing the branchial region instead of the two in *R. sublitoralis*. All other species of *Rhinolambrus* have branchial processes and are therefore clearly distinct from *R. sublitoralis*. There is some similarity between the new species and *Platylambrus serratus* (H. Milne Edwards, 1834) from the Recent of the 'Indian Ocean' [*recte* west Central America, see Rathbun, 1925: 516], but the latter has the hinder part of the posterolateral margins more concave and there are a greater number of tubercles on the anterior part of the posterolateral margins.

Superfamily **LEUCOSIOIDEA** Samouelle, 1819

Family **LEUCOSIIDAE** Samouelle, 1819

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The hepatic and lateral part of the cervical furrows are present as vague lines between the granules; the grooves separating the urogastric and cardiac lobes from one another and from the branchial regions, however, are more clearly defined. The mesogastric lobe is discernible rather by the grouping of granules than by any clear-cut groove. The cardiac is broader than the mesogastric lobe and more or less shield-shaped; it very slightly indents the urogastric in front and probably almost touches the posterior margin behind.

The entire dorsal surface is densely covered in flattened granules of several diameters extending over the rounded lateral edges and sides.

There is a fine groove above the subtriangular pterygostomian region; the outer shell surface near the front is missing: had it been preserved, this part of the region would in all probability have been visible in dorsal view. Oviducts open into fifth sternites.

Discussion. See generic discussion.

Genus ***DRACHIELLA*** Guinot *in* Serène & Soh, 1976

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Description. Carapace transversely subovate, length almost 0.8 of the width, widest about midlength; steeply rounded transversely and in side view steeply rounded from behind the front to the cardiac region which forms a second prominence. Distinct furrows extend from the posterolateral angles to the front, at which point they are separated by the ridged anterior mesogastric process; lobulate marginal tubercles completely isolated from all the dorsal regions. There is a deep indentation between paired tubercles at the lateral angles and one on the anterolateral margins. The straight posterolateral margins have a tubercle behind the lateral pair and another just before the ridged intestinal lobe. The intestinal lobe overhangs and gives a false impression of the posterior margin from which it is separated by a fine groove. From the anterolateral tubercle a short concave tuberculate ridge leads to the outer angle of the orbit. A thin ridge of four to five granules forms the upper orbital margin barely divided from the narrow, almost straight, bluntly depressed front. A groove leading back from the front separates prominent frontal lobes joined behind by the anterior mesogastric process. The very small circular orbits are directed obliquely upwards and divided by a strong septum from somewhat larger, deeper antennal fossae. The epistome appears to have been narrow and acutely V-shaped.

The cervical furrow is obtuse and very shallow where it

crosses the midline about mid-carapace length; becoming much broader, it turns abruptly forwards and outwards to the lateral margin; crossing the margin it divides a lineal subhepatic lobe and a stronger, tapering ridge on the pterygostomian region. A furrow separates obliquely inclined elliptical epigastric lobes from fairly large quadrate hepatic and triangular protogastric lobes; the latter barely separated from one another by an ill-defined furrow. A strong furrow separates the circular cardiac region from the intestinal lobe. Large epibranchial lobes are separated by a furrow (containing a row of tubercles extending from the smaller mesobranchial lobes to the cervical furrow) from a thin, rather sinuous metabranchial lobe.

Bilaterally arranged tubercles of several diameters crowd the dorsal surface; one, more conspicuous, is set behind each upper orbital margin. The more prominent of the cardiac tubercles form a saltire anteriorly with a row at its base, the whole surrounded by a ring of granules. Deep in the grooves many of the tubercles are entire – a few almost mammillate – but the vast majority are cratered with a single median granule.

The buccal margin tapers towards the front and its margin forms a line with the outer orbital margin. The pleural suture is bordered with a line of very small cratered granules while others similar to those on the dorsal surface tend to form rows on the branchiostegite. The abdominal trough is ovate and each sternite has a tubercle at its lateral edge.

Discussion. The four species assigned by Guinot to the genus *Drachiella, D. sculpta, D. morum* Alcock, 1896, *D. lapillula* Alcock, 1896 and *D. aglypha* Laurie, 1906 have the branchial region entire. *D. guinotae* appears to show the primitive condition in which the subdivisions of the branchial region are defined by furrows. The protogastric, epigastric, hepatic, cardiac and intestinal regions are similarly defined by furrows. The furrow separating the hepatic from the protogastric regions is less strongly impressed than the others. The frontal region of *D. guinotae* is less wide (*trans.*) than it is in *D. morum*, and the eyes are more anteriorly situated, and therefore less visible, than in *D. morum*, but more so than in *D. lapillula*.

Genus ***IPHICULUS*** Adams & White, 1848

Type species. By monotypy *Iphiculus spongiosus* Adams & White, 1848 [ICZN Opinion 73], from Recent of the Phillipine Islands.

Range. Pliocene to Recent.

Iphiculus granulatus sp. nov. Figs 15, 16, 18

Diagnosis. Carapace subovate with a granulated dorsal surface; no tubercles developed on the pterygostomian region.

Name. 'Granulated'.

Holotype. In 61868 (♀, Figs 15a–c). Paratype In 61869 (Figs 16, 18). All from locality S.4807, Seria Formation.

Description. The outline of the carapace is closely similar to that of *Iphiculus miriensis* sp. nov. (below), but there is no overshadowing tubercle on the pterygostomian region, which is somewhat less tumid. The orbitofrontal margin is not well preserved; it occupies about two-fifths of the carapace width. The rostrum is sulcate and there are two notches in the thin, upturned upper orbital margin.

With the exception of a narrow depression behind the front and the bases of the median furrows the dorsal surface is densely crowded with granules of several diameters.

The pleural suture is lined with granules and the underside of both sexes is similar to that of *Iphiculus miriensis* sp. nov.

Iphiculus miriensis sp. nov. Figs 11–14

Diagnosis. Carapace subovate with six blunt spines on the lateral margins; the dorsal surface is ornamented with 25 small, regularly arranged tubercles.

Name. 'From Miri'.

Holotype. In 62123 (Fig. 11). Paratypes In 62124–6 (Figs 12–14), In 62127 (♂), In 62128–30 (♀), In 62132–8 (indet. sex). All from locality S.5548, Lower Miri Formation. Paratypes In 62139–43 from S.5549, In 62144 from S.5550, all from Lower Miri Formation. Paratypes In 62121–2 from S.5539, Upper Miri Formation.

Description. The carapace is subovate in outline, the length being about 0.8 of the width measured between the 2nd–3rd lateral spines; longitudinally it is domed with a shallow frontal depression, and flatly domed transversely. The well-rounded anterolateral margins are armed with four blunt spines increasing in size posteriorly; the anterior one is often obscure, almost granular, and overshadowed by a large spine immediately below on the pterygostomian process. The posterolateral margins are longer than the anterolateral margins; there are two granular spines, more noticeable on young specimens, and the space between them is twice the distance which separates the foremost from the spine at the lateral angle, and the hindmost from a short, sharp spine at the posterior angle. The posterior margin is about as wide as the front, slightly concave and narrowly rimmed. The very narrow, slightly upturned front occupies about one third of the carapace width; the rostrum is small, triangular and strongly deflected downwards; the margins are upturned by a continuation of the upper orbital margins, in which there are two notches. The narrowly ovate orbits are inclined about 45° to the midline and partially separated from rather large, subcircular antennal fossae.

The cervical furrow can just be traced on some specimens; it runs slightly back for a short distance from the margin before terminating in a shallow pit, where it joins an obscure, partially developed furrow curving from the outer orbital notch and delineating the hepatic region. A broad groove separates the confluent median gastric and cardiac regions from the large, tumid intestinal region. Broad, but shallow, furrows separate the cardiac and intestinal regions from the branchial regions. There are normally 25 small tubercles on the carapace in all. There are four on each protogastric lobe, the foremost pair forming an upturned curving row with one on each hepatic region, and the hinder pair, a downward curving row with one on each epibranchial lobe; a shorter row is composed of one tubercle on each meso- and metabranchial lobe, while another two, one behind the other, on the metabranchials lie opposite two transverse cardiac tubercles; the urogastric lobe has three tubercles in an inverted triangle. Each tubercle is ringed by, and covered with, small pustular granules, while numerous granules of several diameters are scattered over the elevated parts of the carapace and extend onto the lateral spines.

crosses the midline about mid-carapace length; becoming much broader, it turns abruptly forwards and outwards to the lateral margin; crossing the margin it divides a lineal subhepatic lobe and a stronger, tapering ridge on the pterygostomian region. A furrow separates obliquely inclined elliptical epigastric lobes from fairly large quadrate hepatic and triangular protogastric lobes; the latter barely separated from one another by an ill-defined furrow. A strong furrow separates the circular cardiac region from the intestinal lobe. Large epibranchial lobes are separated by a furrow (containing a row of tubercles extending from the smaller mesobranchial lobes to the cervical furrow) from a thin, rather sinuous metabranchial lobe.

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The buccal margin tapers towards the front and its margin forms a line with the outer orbital margin. The pleural suture is bordered with a line of very small cratered granules while others similar to those on the dorsal surface tend to form rows on the branchiostegite. The abdominal trough is ovate and each sternite has a tubercle at its lateral edge.

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RANGE. Pliocene to Recent.

Iphiculus granulatus sp. nov. Figs 15, 16, 18

DIAGNOSIS. Carapace subovate with a granulated dorsal surface; no tubercles developed on the pterygostomian region.

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Iphiculus miriensis sp. nov. Figs 11–14

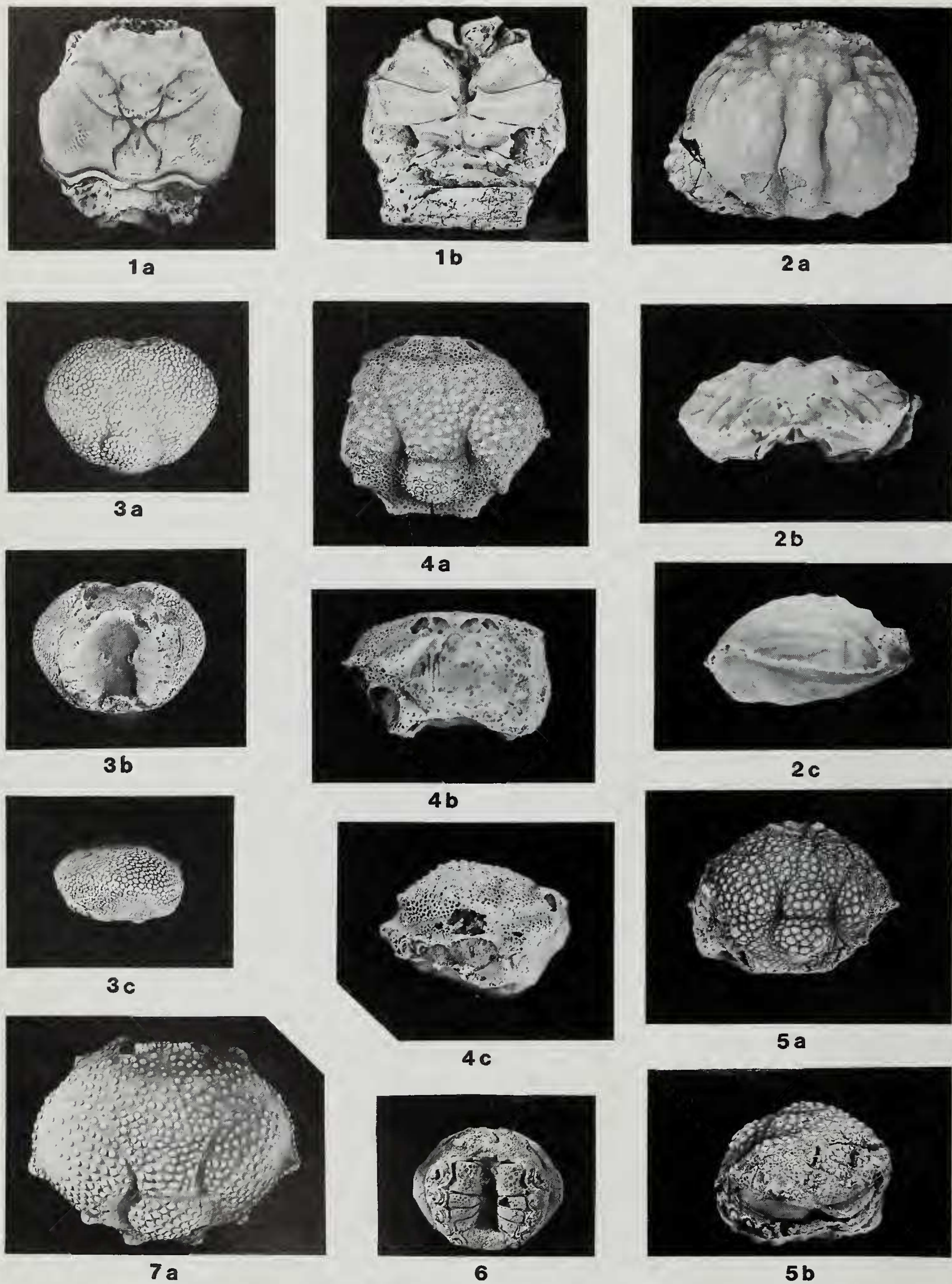
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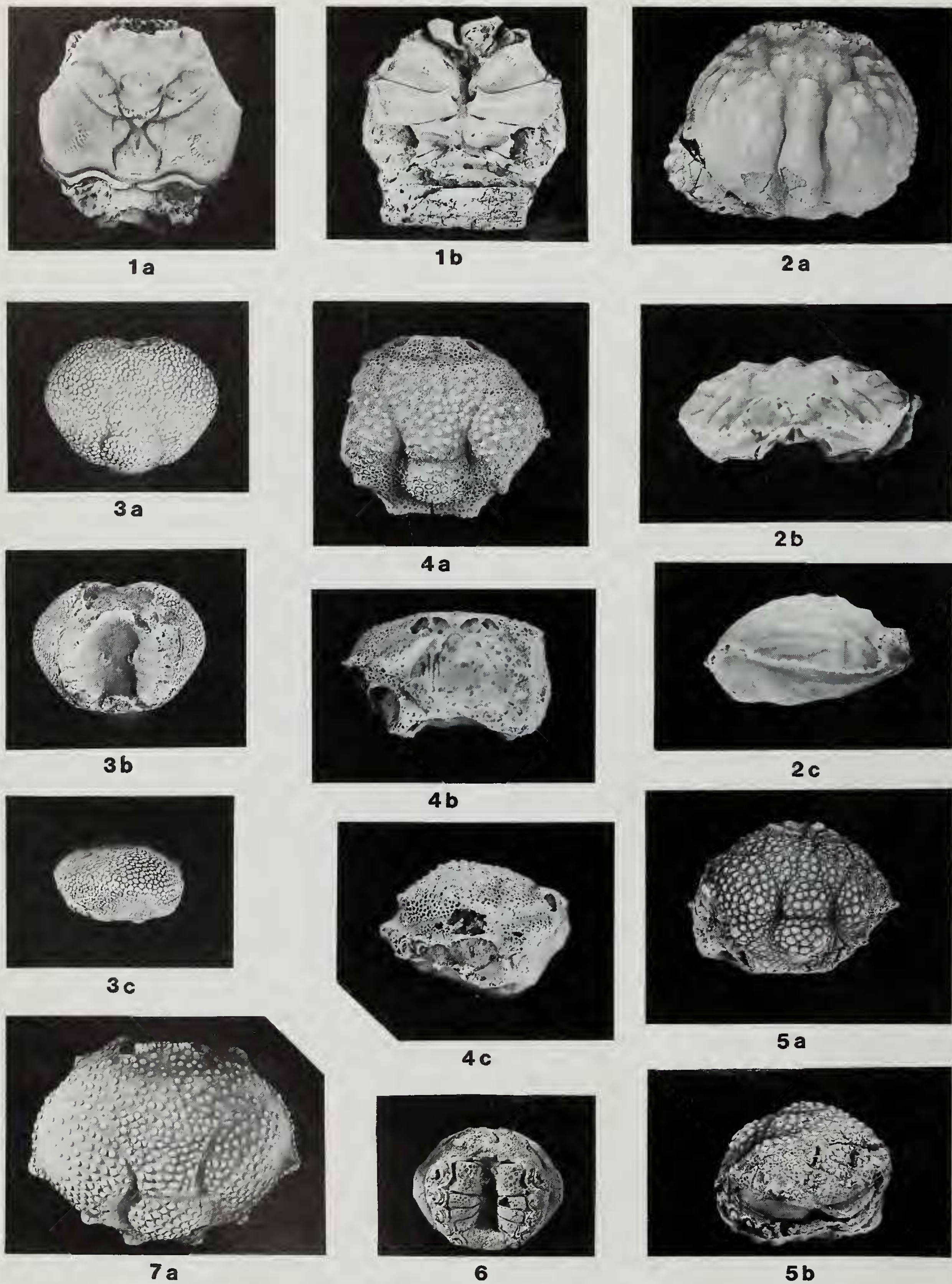
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1a
1b
2a
3a
4a
2b
3b
4b
2c
3c
4c
5a
7a
6
5b


1a
1b
2a
3a
4a
2b
3b
4b
2c
3c
4c
5a
7a
6
5b

A row of granules generally lines the pleural suture, and the pterygostomian region is well delimited and tumid. The branchiostegite becomes devoid of granules posteriorly. The buccal margins are straight and divergent.

Of the sternites, the 1st and 2nd are reduced to a narrow transverse ridge with a median granular prominence; the 3rd and 4th sternites are triangular and of similar size, while the 5th–8th are subrectangular and decrease in size posteriorly.

In the male the abdominal trough extends almost the full length of the 3rd sternites and the deep, steep-sided walls are ridged above by a line of coarse granules. This ridge is not developed in the female in which the abdominal trough is broadly concave and, except anteriorly, the sternites are less studded with granules.

Iphiculus sexspinosus sp. nov. Figs 17, 19

DIAGNOSIS. Carapace subovate with six marginal spines and a prominent pterygostomian tubercle; the cardiac and intestinal tubercles are vestigial and the dorsal tubercles are restricted to two transverse rows anteriorly.

NAME. 'Six-spined.'

HOLOTYPE. In 61864 (♂, Figs 17a, b) from locality S.5536, Seria Formation. Paratypes In 61865 (Fig. 19), In 61866 from S.5539, Upper Miri Formation; In 61867 from S.5537, Seria Formation.

DESCRIPTION. The outline of the carapace and its marginal spines is essentially similar to that of *Iphiculus miriensis* sp. nov. (p. 11). The front is slightly produced; the tip of the rostrum is obscured, but behind it is sharply divided medially by a deep V-shaped cleft which continues back a short way onto the carapace. The upper orbital margin is formed by three short equidistant spines, deeply divided by notches; the median spine is directed a little upwards.

The cardiac and intestinal tubercles are not seen on the outer shell surface, although they are vestigially present as structures on an inner-shell layer; the other dorsal tubercles are much reduced in size and tend to be restricted to two anteriorly distributed rows each comprising six tubercles.

DISCUSSION. Of the present collection *I. sexspinosus* probably comes closest to the type species *I. spongiosus*, the latter having a rather coarser surface ornament and only a single line of vague 'tubercles' corresponding to the posterior row on *I. sexspinosus*. The long lateral spine typical of *I. spongiosus* reaches a length of about a fifth of the carapace width, whilst in *I. granulatus* it would probably have reached about a quarter of the carapace width. The granulation of *I. granulatus* sp. nov. (p. 11) is coarser than that of *I. sexspinosus*, and the secondary tubercular ornament is wanting; the cardiac region is less well defined. The greater number and larger size of secondary tubercles distinguishes *I. miriensis* from *I. sexspinosus*.

Genus ***LEUCOSIA*** Weber, 1795

TYPE SPECIES. By subsequent designation of Holthuis, 1959: *Cancer craniolaris* Linnaeus, 1758 [ICZN Opinion 712]; from Recent of the Indo-Pacific.

RANGE. Miocene to Recent.

REMARKS. The International Commission on Zoological Nomenclature appears to have overlooked the selection by H. Milne Edwards (October, 1837: pl. 25, fig. 1) of *Leucosia urania* Fabricius, 1798 as type species.

Leucosia longiangulata sp. nov. Figs 25, 26

DIAGNOSIS. The carapace is broadly rhomboidal with a narrow, slightly produced front and thin, elongate lateral angles; the deep thoracic sinus terminates in a pit from which a groove extends to the lateral margin.

NAME. From Latin *longus*, long + *angulatus*, with angles.

HOLOTYPE. In 61890 (Figs 25, 26) from locality S.10474, Lower Miri Formation.

DESCRIPTION. The carapace is rhomboidal in outline, about one-seventh longer than wide and much narrowed anteriorly. The front is slightly produced, vaguely tridentate with the sharply downturned rostrum taking up the middle third; the triangular elevation above is rounded. There is very little constriction behind the front and the gently convex anterolateral margins lead to rather elongate lateral angles, commencing about one third distant from the front. The lateral edge is sharp and finely granulated, the granules continuing only a short distance beyond the lateral angles. The posterolateral margins are a little recurved before acute posterior angles. The posterior margin is somewhat extended, flattened, straight and bordered with granules; it is about twice the frontal width.

The thoracic sinus is deep and ends well in front of the 1st limbs in a rather deep, obtusely ovate pit which has a narrow groove passing upward round the lateral edge immediately before the lateral angle.

DISCUSSION. See p. 15.

Leucosia serenei sp. nov. Figs 20–23

DIAGNOSIS. The carapace is rhomboidal with the front moderately produced and narrow; the thoracic sinus is broad and terminates in an obscure depression.

NAME. In honour of Dr Raoul Serène.

HOLOTYPE. In 61870 (Figs 20a–b). Paratypes In 61871 (Fig. 21), In 61872 (Fig. 22), In 61873 (Fig. 23), In 61874–80. All from locality S.5548, Lower Miri Formation. Paratypes In 61881–4 from S.5539, Upper Miri Formation.

Fig. 1 *Dorippe frascone tuberculata* subsp. nov. **Holotype** In 61853 from S.5548, Lower Miri Formation, × 1. a, dorsal view; b, ventral view.
Fig. 2 *Calappa sexaspinosa* sp. nov. **Holotype** In 61857 from S.5548, Lower Miri Formation, × 3. a, dorsal view; b, right lateral view; c, anterior view.
Fig. 3 *Ampliura simplex* gen. et sp. nov. **Holotype** In 62157 from S.5537, Seria Formation, × 5. a, dorsal view; b, ventral view; c, right lateral view.
Fig. 4 *Nucia borneoensis* sp. nov. **Holotype** In 62145 from S.5548, Lower Miri Formation, × 4. a, dorsal view; b, anterior view; c, right lateral view.
Figs 5, 6 *Nucia borneoensis* sp. nov. Fig. 5, paratype In 62148 from S.10475, Lower Miri Formation, × 4. a, dorsal view; b, right lateral view. Fig. 6, ventral view of paratype In 62146 from S.5548, Lower Miri Formation, × 3.
Fig. 7a *Typilobus marginatus* sp. nov. Dorsal view of **holotype** In 62163 from NB 11541, Middle Miocene, Tungku Formation, × 3. See also Figs 7b–d (p. 14).

A row of granules generally lines the pleural suture, and the pterygostomian region is well delimited and tumid. The branchiostegite becomes devoid of granules posteriorly. The buccal margins are straight and divergent.

Of the sternites, the 1st and 2nd are reduced to a narrow transverse ridge with a median granular prominence; the 3rd and 4th sternites are triangular and of similar size, while the 5th–8th are subrectangular and decrease in size posteriorly.

In the male the abdominal trough extends almost the full length of the 3rd sternites and the deep, steep-sided walls are ridged above by a line of coarse granules. This ridge is not developed in the female in which the abdominal trough is broadly concave and, except anteriorly, the sternites are less studded with granules.

Iphiculus sexspinosus sp. nov. Figs 17, 19

Diagnosis. Carapace subovate with six marginal spines and a prominent pterygostomian tubercle; the cardiac and intestinal tubercles are vestigial and the dorsal tubercles are restricted to two transverse rows anteriorly.

Name. 'Six-spined.'

Holotype. In 61864 (♂, Figs 17a, b) from locality S.5536, Seria Formation. Paratypes In 61865 (Fig. 19), In 61866 from S.5539, Upper Miri Formation; In 61867 from S.5537, Seria Formation.

Description. The outline of the carapace and its marginal spines is essentially similar to that of *Iphiculus miriensis* sp. nov. (p. 11). The front is slightly produced; the tip of the rostrum is obscured, but behind it is sharply divided medially by a deep V-shaped cleft which continues back a short way onto the carapace. The upper orbital margin is formed by three short equidistant spines, deeply divided by notches; the median spine is directed a little upwards.

The cardiac and intestinal tubercles are not seen on the outer shell surface, although they are vestigially present as structures on an inner-shell layer; the other dorsal tubercles are much reduced in size and tend to be restricted to two anteriorly distributed rows each comprising six tubercles.

Discussion. Of the present collection *I. sexspinosus* probably comes closest to the type species *I. spongiosus*, the latter having a rather coarser surface ornament and only a single line of vague 'tubercles' corresponding to the posterior row on *I. sexspinosus*. The long lateral spine typical of *I. spongiosus* reaches a length of about a fifth of the carapace width, whilst in *I. granulatus* it would probably have reached about a quarter of the carapace width. The granulation of *I. granulatus* sp. nov. (p. 11) is coarser than that of *I. sexspinosus*, and the secondary tubercular ornament is wanting; the cardiac region is less well defined. The greater number and larger size of secondary tubercles distinguishes *I. miriensis* from *I. sexspinosus*.

Genus *LEUCOSIA* Weber, 1795

Type species. By subsequent designation of Holthuis, 1959: *Cancer craniolaris* Linnaeus, 1758 [ICZN Opinion 712]; from Recent of the Indo-Pacific.

Range. Miocene to Recent.

Remarks. The International Commission on Zoological Nomenclature appears to have overlooked the selection by H. Milne Edwards (October, 1837: pl. 25, fig. 1) of *Leucosia urania* Fabricius, 1798 as type species.

Leucosia longiangulata sp. nov. Figs 25, 26

Diagnosis. The carapace is broadly rhomboidal with a narrow, slightly produced front and thin, elongate lateral angles; the deep thoracic sinus terminates in a pit from which a groove extends to the lateral margin.

Name. From Latin *longus*, long + *angulatus*, with angles.

Holotype. In 61890 (Figs 25, 26) from locality S.10474, Lower Miri Formation.

Description. The carapace is rhomboidal in outline, about one-seventh longer than wide and much narrowed anteriorly. The front is slightly produced, vaguely tridentate with the sharply downturned rostrum taking up the middle third; the triangular elevation above is rounded. There is very little constriction behind the front and the gently convex anterolateral margins lead to rather elongate lateral angles, commencing about one third distant from the front. The lateral edge is sharp and finely granulated, the granules continuing only a short distance beyond the lateral angles. The posterolateral margins are a little recurved before acute posterior angles. The posterior margin is somewhat extended, flattened, straight and bordered with granules; it is about twice the frontal width.

The thoracic sinus is deep and ends well in front of the 1st limbs in a rather deep, obtusely ovate pit which has a narrow groove passing upward round the lateral edge immediately before the lateral angle.

Discussion. See p. 15.

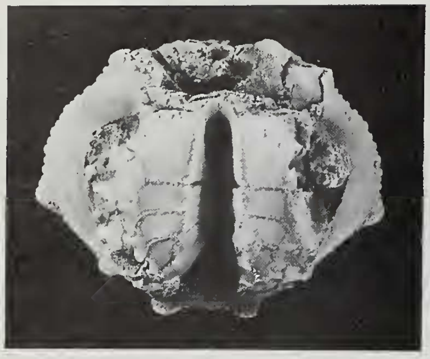
Leucosia serenei sp. nov. Figs 20–23

Diagnosis. The carapace is rhomboidal with the front moderately produced and narrow; the thoracic sinus is broad and terminates in an obscure depression.

Name. In honour of Dr Raoul Serène.

Holotype. In 61870 (Figs 20a–b). Paratypes In 61871 (Fig. 21), In 61872 (Fig. 22), In 61873 (Fig. 23), In 61874–80. All from locality S.5548, Lower Miri Formation. Paratypes In 61881–4 from S.5539, Upper Miri Formation.

Fig. 1 *Dorippe frascone tuberculata* subsp. nov. **Holotype** In 61853 from S.5548, Lower Miri Formation, × 1. a, dorsal view; b, ventral view.
Fig. 2 *Calappa sexaspinosa* sp. nov. **Holotype** In 61857 from S.5548, Lower Miri Formation, × 3. a, dorsal view; b, right lateral view; c, anterior view.
Fig. 3 *Ampliura simplex* gen. et sp. nov. **Holotype** In 62157 from S.5537, Seria Formation, × 5. a, dorsal view; b, ventral view; c, right lateral view.
Fig. 4 *Nucia borneoensis* sp. nov. **Holotype** In 62145 from S.5548, Lower Miri Formation, × 4. a, dorsal view; b, anterior view; c, right lateral view.
Figs 5, 6 *Nucia borneoensis* sp. nov. Fig. 5, paratype In 62148 from S.10475, Lower Miri Formation, × 4. a, dorsal view; b, right lateral view. Fig. 6, ventral view of paratype In 62146 from S.5548, Lower Miri Formation, × 3.
Fig. 7a *Typilobus marginatus* sp. nov. Dorsal view of **holotype** In 62163 from NB 11541, Middle Miocene, Tungku Formation, × 3. See also Figs 7b–d (p. 14).



7b



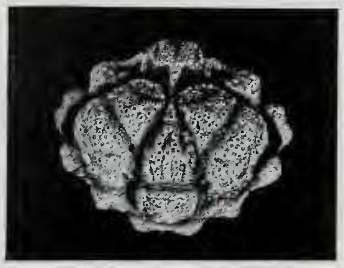
7c



7d



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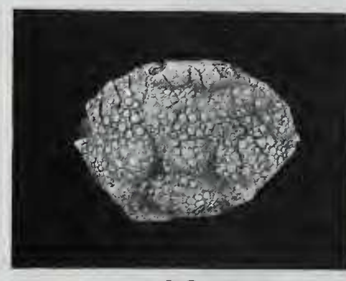
9a



9b



9c



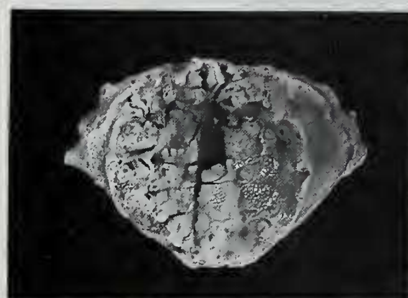
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11



13



14



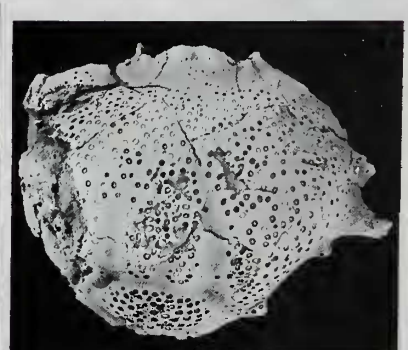
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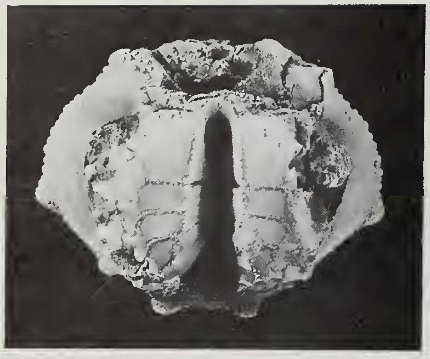
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15b



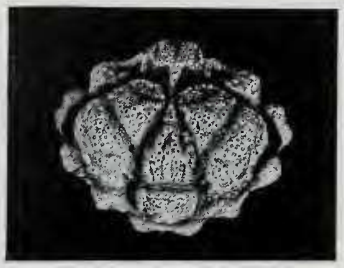
15a


7b


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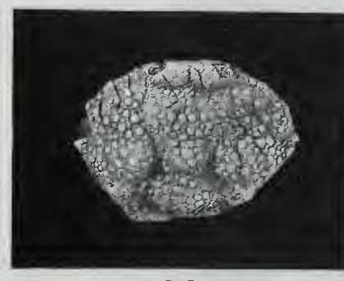

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9a

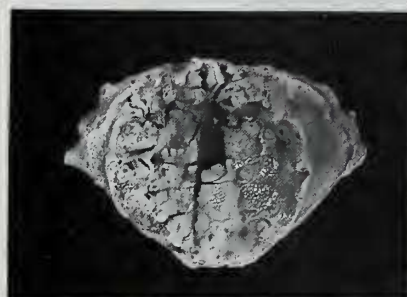

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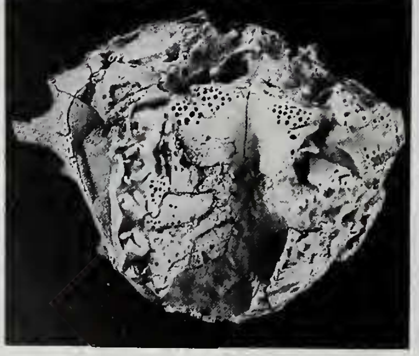

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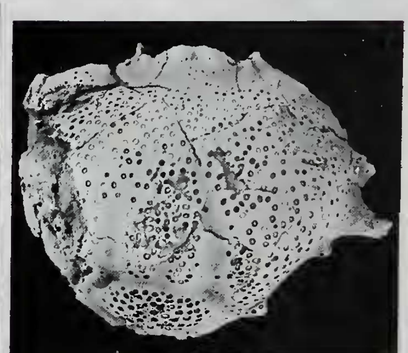

13


14


12


15c


15b


15a

DESCRIPTION. The carapace is rhomboidal in outline, about one-sixth longer than wide and much narrowed anteriorly. The front is moderately produced and the narrow triangular elevation above it is somewhat flattened and extends back a short distance. There is a very shallow depression either side of the front and the convex anterolateral margins are constricted again immediately before the broadly rounded lateral angles, set at some three-fifths the distance from the front. The margin is sharp and finely granulate, with the granules becoming sparser as they extend above the posterolateral margin as far as the posterior angles. The posterolateral margins converge to shallow incisions for the 5th coxae; the posterior margin is about twice the width of the front, nearly straight and bounded by a narrow, almost smooth ridge.

The thoracic sinus is very broad and ends in an obscure depression just in front of the first limb; there are a few minute granules scattered within the depression and a few others line its lower margin.

Internal moulds show low granular 'ridges' flanking an obscure median 'ridge' on the gastric region, and there is a group of three granules set in an inverted triangle on the cardiac region.

On the male abdomen somites 3–5 are fused and together equal the length of the 6th somite; the 3rd–5th somites of the female are very narrow, while the 6th occupies almost all the sternal area. In both sexes the telson is much reduced in size and extends well into the 3rd sternites.

DISCUSSION. See below.

Leucosia tutongensis sp. nov. Fig. 24

DIAGNOSIS. The carapace is rhomboidal with the front not much produced; the broad, shallow thoracic sinus terminates in a deep pit.

NAME. 'From Tutong'.

HOLOTYPE. In 61885 (Figs 24a–c) from locality S.5539, Upper Miri Formation. Paratypes In 61886 from S.5544, Lower Miri Formation and In 61887–9 from S.5548, Lower Miri Formation.

DESCRIPTION. The carapace is similar in outline to *Leucosia serenei* but about one-fifth longer than wide. The front is not much produced and the triangular elevation above is rounded and extends a short distance back. There is a shallow depression on either side of the front and the weakly convex anterolateral margins lead to narrowly rounded lateral angles set at about mid-carapace length. From the lateral angle a minutely granulated ridge, continuous with the anterolateral margin, extends back onto the branchial region to about as far as the 3rd pair of limbs; the true posterolateral margin is finely granulate, weakly incised for the 5th limb and leads by way of acute posterior angles to the posterior margin which is straight to weakly convex and finely granulated.

The broad, rather shallow thoracic sinus ends in a deep ovate pit just in front of the insertion of the 1st limb; a few fine granules line the lower margin of the sulcus and there is a scattering of minute granules within the pit.

Deep wedge-shaped gonopores open into the abdominal cleft at the 5th sternites and are bounded behind by a narrow, wall-like process extending from the 6th sternites (Fig. 24c). The abdomen of the male is similar to that of *Leucosia serenei*.

DISCUSSION of the species of *Leucosia*. The carapace width of *Leucosia longiangulata* sp. nov. is greater in relation to length than either *Leucosia serenei* sp. nov. or *Leucosia tutongensis* sp. nov.; it may be further distinguished by the elongate, forwardly situated lateral angle, by the deep thoracic sinus and the groove extending from it to the lateral edge. *L. longiangulata* compares well with *L. vittata* Stimpson, 1858, but the thoracic sinus is much further forward, hence the maximum width is also much further forward. It compares best with *L. serenei* sp. nov., but the thoracic sinus in the latter species does not reach the upper margin.

The subcarinate transverse section of *L. serenei* compares by and large with that of *Leucosia obscura* Bell, 1855, Recent of the Philippine Islands, but the latter species is a little broader with a narrow thoracic sinus terminating in a double notch, rather than broad and terminating in a depression as in *L. serenei*. *L. tutongensis* superficially resembles the Recent widespread Indo-Pacific *Leucosia longifrons* de Haan, 1841.

Genus *MYRA* Leach, 1817

TYPE SPECIES. By monotypy *Leucosia fugax* Fabricius, 1798 [ICZN Opinion 712]; from Recent of the Indo-Pacific Region.

RANGE. Miocene to Recent.

Myra brevisulcata sp. nov. Fig. 29

DIAGNOSIS. The carapace is subovate with laterally developed shallow cervical furrows; the anterolateral margin is represented by a cluster, rather than a line, of granules; larger granules are scattered over an otherwise minutely granulated surface.

NAME. 'With short furrows'

HOLOTYPE. In 61900 (Fig. 29) from locality S.10474, Lower Miri Formation.

DESCRIPTION. The carapace is subglobose with three moderately stout sharp spines, one at each posterior angle and a larger median one just above the posterior margin. The length excluding the spine slightly exceeds the breadth; it is widest at about midlength. Details of the slightly ascending front are not preserved. The outer wall of the hepatic region,

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Fig. 7b–d *Typilobus marginatus* sp. nov. **Holotype** In 62163 from NB 11541, Middle Miocene, Tungku Formation, × 3. b, ventral view; c, right lateral view; d, anterior view. See also Fig. 7a (p. 12).

Fig. 8 *Typilobus* sp. Dorsal view of abraded specimen In 46373 from NB 132, ?Lower Miocene, Simengaris Formation, × 6.

Fig. 9 *Drachiella guinotae* sp. nov. **Holotype** In 61863 from S.10475, Lower Miri Formation, × 2. a, dorsal view; b, ventral view; c, anterior view.

Fig. 10 *Nucia calculoides* sp. nov. **Holotype** In 62158 from S.10474, Lower Miri Formation, × 3.

Figs 11–14 *Iphiculus miriensis* sp. nov. Locality S.5548, Lower Miri Formation. Fig. 11, dorsal view of **holotype** (♂) In 62123, × 2. Fig. 12, ventral view of paratype (♀) In 62124, × 3. Fig. 13, ventral view of paratype (♂) In 62125. Fig. 14, ventral view of paratype (♂) In 62126, × 3.

Fig. 15 *Iphiculus granulatus* sp. nov. **Holotype** (♀) In 61868 from Penanjong, Seria Formation, × 3. a–c, dorsal, ventral and anterior views.

DESCRIPTION. The carapace is rhomboidal in outline, about one-sixth longer than wide and much narrowed anteriorly. The front is moderately produced and the narrow triangular elevation above it is somewhat flattened and extends back a short distance. There is a very shallow depression either side of the front and the convex anterolateral margins are constricted again immediately before the broadly rounded lateral angles, set at some three-fifths the distance from the front. The margin is sharp and finely granulate, with the granules becoming sparser as they extend above the posterolateral margin as far as the posterior angles. The posterolateral margins converge to shallow incisions for the 5th coxae; the posterior margin is about twice the width of the front, nearly straight and bounded by a narrow, almost smooth ridge.

The thoracic sinus is very broad and ends in an obscure depression just in front of the first limb; there are a few minute granules scattered within the depression and a few others line its lower margin.

Internal moulds show low granular 'ridges' flanking an obscure median 'ridge' on the gastric region, and there is a group of three granules set in an inverted triangle on the cardiac region.

On the male abdomen somites 3–5 are fused and together equal the length of the 6th somite; the 3rd–5th somites of the female are very narrow, while the 6th occupies almost all the sternal area. In both sexes the telson is much reduced in size and extends well into the 3rd sternites.

DISCUSSION. See below.

Leucosia tutongensis sp. nov. Fig. 24

DIAGNOSIS. The carapace is rhomboidal with the front not much produced; the broad, shallow thoracic sinus terminates in a deep pit.

NAME. 'From Tutong'.

HOLOTYPE. In 61885 (Figs 24a–c) from locality S.5539, Upper Miri Formation. Paratypes In 61886 from S.5544, Lower Miri Formation and In 61887–9 from S.5548, Lower Miri Formation.

DESCRIPTION. The carapace is similar in outline to *Leucosia serenei* but about one-fifth longer than wide. The front is not much produced and the triangular elevation above is rounded and extends a short distance back. There is a shallow depression on either side of the front and the weakly convex anterolateral margins lead to narrowly rounded lateral angles set at about mid-carapace length. From the lateral angle a minutely granulated ridge, continuous with the anterolateral margin, extends back onto the branchial region to about as far as the 3rd pair of limbs; the true posterolateral margin is finely granulate, weakly incised for the 5th limb and leads by way of acute posterior angles to the posterior margin which is straight to weakly convex and finely granulated.

The broad, rather shallow thoracic sinus ends in a deep ovate pit just in front of the insertion of the 1st limb; a few fine granules line the lower margin of the sulcus and there is a scattering of minute granules within the pit.

Deep wedge-shaped gonopores open into the abdominal cleft at the 5th sternites and are bounded behind by a narrow, wall-like process extending from the 6th sternites (Fig. 24c). The abdomen of the male is similar to that of *Leucosia serenei*.

DISCUSSION of the species of *Leucosia*. The carapace width of *Leucosia longiangulata* sp. nov. is greater in relation to length than either *Leucosia serenei* sp. nov. or *Leucosia tutongensis* sp. nov.; it may be further distinguished by the elongate, forwardly situated lateral angle, by the deep thoracic sinus and the groove extending from it to the lateral edge. *L. longiangulata* compares well with *L. vittata* Stimpson, 1858, but the thoracic sinus is much further forward, hence the maximum width is also much further forward. It compares best with *L. serenei* sp. nov., but the thoracic sinus in the latter species does not reach the upper margin.

The subcarinate transverse section of *L. serenei* compares by and large with that of *Leucosia obscura* Bell, 1855, Recent of the Philippine Islands, but the latter species is a little broader with a narrow thoracic sinus terminating in a double notch, rather than broad and terminating in a depression as in *L. serenei*. *L. tutongensis* superficially resembles the Recent widespread Indo-Pacific *Leucosia longifrons* de Haan, 1841.

Genus *MYRA* Leach, 1817

TYPE SPECIES. By monotypy *Leucosia fugax* Fabricius, 1798 [ICZN Opinion 712]; from Recent of the Indo-Pacific Region.

RANGE. Miocene to Recent.

Myra brevisulcata sp. nov. Fig. 29

DIAGNOSIS. The carapace is subovate with laterally developed shallow cervical furrows; the anterolateral margin is represented by a cluster, rather than a line, of granules; larger granules are scattered over an otherwise minutely granulated surface.

NAME. 'With short furrows'

HOLOTYPE. In 61900 (Fig. 29) from locality S.10474, Lower Miri Formation.

DESCRIPTION. The carapace is subglobose with three moderately stout sharp spines, one at each posterior angle and a larger median one just above the posterior margin. The length excluding the spine slightly exceeds the breadth; it is widest at about midlength. Details of the slightly ascending front are not preserved. The outer wall of the hepatic region,

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Fig. 7b–d *Typilobus marginatus* sp. nov. **Holotype** In 62163 from NB 11541, Middle Miocene, Tungku Formation, × 3. b, ventral view; c, right lateral view; d, anterior view. See also Fig. 7a (p. 12).

Fig. 8 *Typilobus* sp. Dorsal view of abraded specimen In 46373 from NB 132, ?Lower Miocene, Simengaris Formation, × 6.

Fig. 9 *Drachiella guinotae* sp. nov. **Holotype** In 61863 from S.10475, Lower Miri Formation, × 2. a, dorsal view; b, ventral view; c, anterior view.

Fig. 10 *Nucia calculoides* sp. nov. **Holotype** In 62158 from S.10474, Lower Miri Formation, × 3.

Figs 11–14 *Iphiculus miriensis* sp. nov. Locality S.5548, Lower Miri Formation. Fig. 11, dorsal view of **holotype** (♂) In 62123, × 2. Fig. 12, ventral view of paratype (♀) In 62124, × 3. Fig. 13, ventral view of paratype (♂) In 62125. Fig. 14, ventral view of paratype (♂) In 62126, × 3.

Fig. 15 *Iphiculus granulatus* sp. nov. **Holotype** (♀) In 61868 from Penanjong, Seria Formation, × 3. a–c, dorsal, ventral and anterior views.

forming the apparent anterolateral margin, is well rounded, ridged and granulated with finer granules interspersed; it terminates in a shallow pit in which the granules are minute and confined to the upper posterior wall. A line of granules overlapping the ridge passes over the pit and continues back to form the posterolateral margin, which is sharp. Its demarcating line of granules becomes finer and runs back almost as far as the middle of the cardiac region and limits the upward extent of a densely granulated area. A low, rounded ridge with scattered granules, representing the anterolateral margin, extends between the front to above the marginal pit. The cervical furrows are present as broad lateral depressions curving forward round the foregoing ridge to become obsolete just above the anterior granules of the posterolateral margins.

A few scattered granules occur on an otherwise finely pitted dorsal surface.

DISCUSSION. The extension of the posterolateral margin over the marginal pit, laterally developed cervical furrows and sparsely granulated dorsal surface, together with the broadest part of the carapace occurring further back, readily distinguish this species from *Myra subcarinata* sp. nov. and *Myra trispinosa* sp. nov.

Myra subcarinata sp. nov. Fig. 27

DIAGNOSIS. The carapace is subovate and vaguely carinated; the median is the stoutest of the three posterior spines; the dorsal surface is finely granulated.

NAME. 'Slightly keeled'.

HOLOTYPE. In 61891 (Figs 27a–c) from locality S.5548, Lower Miri Formation. Paratype In 61892 from S.5539, Upper Miri Formation.

DESCRIPTION. The carapace is subglobose, obscurely carinated, with three stout, bluntly rounded spines, one at either angle of the posterior margin, and much the longest a median one just above the posterior margin. Exclusive of the spine, the length just exceeds the breadth. The slightly ascending orbitofrontal margin occupies about one-third of the width and the narrow triangular front is sulcate and downturned at its tip. Behind the orbital angle an angularly convex anterolateral margin is formed by the side wall of the subhepatic region which is continuous with the upper surface of the carapace and lined with a row of granules ending posteriorly in a shallow pit. Behind the pit the posterolateral margin is abruptly convex; it is sharp-edged and lined with granules for about half its length, after which the granules give way and the edge becomes rounded.

The regions are poorly defined. Behind the front, on either side of the midline is a shallow semi-circular depression. An exceedingly fine groove lined with pits separates the cardiac from the gastric regions and shallow depressions, rather than furrows, separate the anterior half of the cardiac from the branchial region.

A little above and anterior to the marginal pit is a granule somewhat larger than those crowding the dorsal surface; the latter tend to form a straggling median line extending to the front. The granules beneath the hepatic lobe and those lining either side of the marginal pit are more variable in size.

DISCUSSION. The shorter, less excavated anterolateral margin and partially granulated posterolateral margin distinguish this species from *M. fugax*.

Myra trispinosa sp. nov. Fig. 28

DIAGNOSIS. The carapace is subovate with three stout posterior spines of which the median is the longest; the anterolateral margins are marked by a line of granules.

NAME. 'Three-spined'.

HOLOTYPE. In 61893 (Figs 28a–c) and paratypes In 61894–5, all from locality S.5548, Lower Miri Formation. Paratypes In 61896–7, from S.5539, Upper Miri Formation; paratypes In 61898–9 from S.5544, Lower Miri Formation.

DESCRIPTION. A large subglobose species with three stout, bluntly rounded spines, one at each posterior angle and a larger median one just above the posterior margin. The length, excluding spine, slightly exceeds the breadth. Details of the front are not preserved. Behind the orbital angle and above the apparent anterolateral margin formed by the outer wall of the sub-hepatic region, the true margin is represented by a short row of granules. The granules lining the hepatic margin become clustered posteriorly and the margin ends in a shallow pit. The posterolateral margin commences above the pit and its sharp, granulated edge extends almost to the posterior margin.

The regions are poorly defined. The anterior wall of the marginal pit is granulated and over the dorsal surface there is a scattering of larger granules among densely crowded minute granules. A subsurface shell layer shows a similar arrangement of pits.

DISCUSSION. *Myra trispinosa* sp. nov. is distinguishable from *M. subcarinata* by the presence of granules forming the anterolateral margin, the posterolateral margin commencing above the marginal pit, and the continued sharp edge of that margin posteriorly.

Genus *NUCIA* Dana, 1852

TYPE SPECIES. By monotypy *Nucia speciosa* Dana, 1852, from Recent of Indo-Pacific.

Figs 16, 18 *Iphiculus granulatus* sp. nov. Paratype (♂) In 61869 from Penanjong, Seria Formation, × 3. Fig. 16, dorsal view; Fig. 18, ventral view.

Fig. 17 *Iphiculus sexspinosus* sp. nov. **Holotype** In 61864 from S.5536, Seria Formation, × 2. a, dorsal view; b, ventral view.

Fig. 19 *Iphiculus sexspinosus* sp. nov. Latex cast of paratype In 61865 from S.5539, Upper Miri Formation, × 2.

Figs 20–23 *Leucosia serenei* sp. nov. from S.5548, Lower Miri Formation. Fig. 20, **holotype** In 61870, × 3. a, b dorsal and right lateral views. Fig. 21, paratype (♂) In 61871, ventral view, × 4. Fig. 22, paratype (♀) In 61872, ventral view, × 3. Fig. 23, paratype (♀) In 61873, ventral view showing the gonopores, × 3.

Fig. 24 *Leucosia tutongensis* sp. nov. **Holotype** (♂) In 61885 from S.5539, Lower Miri Formation, × 3. a, dorsal view; b, ventral view; c, right lateral view showing the gonopores.

Figs 25, 26 *Leucosia longiangulata* sp. nov. **Holotype** In 61890 from S.10474, Lower Miri Formation, × 3. Fig. 25, dorsal view; Fig. 26, right lateral view.

Fig. 27 *Myra subcarinata* sp. nov. **Holotype** In 61891 from S.5548, Lower Miri Formation, × 2. a–c, dorsal, right lateral and anterior views.

forming the apparent anterolateral margin, is well rounded, ridged and granulated with finer granules interspersed; it terminates in a shallow pit in which the granules are minute and confined to the upper posterior wall. A line of granules overlapping the ridge passes over the pit and continues back to form the posterolateral margin, which is sharp. Its demarcating line of granules becomes finer and runs back almost as far as the middle of the cardiac region and limits the upward extent of a densely granulated area. A low, rounded ridge with scattered granules, representing the anterolateral margin, extends between the front to above the marginal pit. The cervical furrows are present as broad lateral depressions curving forward round the foregoing ridge to become obsolete just above the anterior granules of the posterolateral margins.

A few scattered granules occur on an otherwise finely pitted dorsal surface.

DISCUSSION. The extension of the posterolateral margin over the marginal pit, laterally developed cervical furrows and sparsely granulated dorsal surface, together with the broadest part of the carapace occurring further back, readily distinguish this species from *Myra subcarinata* sp. nov. and *Myra trispinosa* sp. nov.

Myra subcarinata sp. nov. Fig. 27

DIAGNOSIS. The carapace is subovate and vaguely carinated; the median is the stoutest of the three posterior spines; the dorsal surface is finely granulated.

NAME. 'Slightly keeled'.

HOLOTYPE. In 61891 (Figs 27a–c) from locality S.5548, Lower Miri Formation. Paratype In 61892 from S.5539, Upper Miri Formation.

DESCRIPTION. The carapace is subglobose, obscurely carinated, with three stout, bluntly rounded spines, one at either angle of the posterior margin, and much the longest a median one just above the posterior margin. Exclusive of the spine, the length just exceeds the breadth. The slightly ascending orbitofrontal margin occupies about one-third of the width and the narrow triangular front is sulcate and downturned at its tip. Behind the orbital angle an angularly convex anterolateral margin is formed by the side wall of the subhepatic region which is continuous with the upper surface of the carapace and lined with a row of granules ending posteriorly in a shallow pit. Behind the pit the posterolateral margin is abruptly convex; it is sharp-edged and lined with granules for about half its length, after which the granules give way and the edge becomes rounded.

The regions are poorly defined. Behind the front, on either side of the midline is a shallow semi-circular depression. An exceedingly fine groove lined with pits separates the cardiac from the gastric regions and shallow depressions, rather than furrows, separate the anterior half of the cardiac from the branchial region.

A little above and anterior to the marginal pit is a granule somewhat larger than those crowding the dorsal surface; the latter tend to form a straggling median line extending to the front. The granules beneath the hepatic lobe and those lining either side of the marginal pit are more variable in size.

DISCUSSION. The shorter, less excavated anterolateral margin and partially granulated posterolateral margin distinguish this species from *M. fugax*.

Myra trispinosa sp. nov. Fig. 28

DIAGNOSIS. The carapace is subovate with three stout posterior spines of which the median is the longest; the anterolateral margins are marked by a line of granules.

NAME. 'Three-spined'.

HOLOTYPE. In 61893 (Figs 28a–c) and paratypes In 61894–5, all from locality S.5548, Lower Miri Formation. Paratypes In 61896–7, from S.5539, Upper Miri Formation; paratypes In 61898–9 from S.5544, Lower Miri Formation.

DESCRIPTION. A large subglobose species with three stout, bluntly rounded spines, one at each posterior angle and a larger median one just above the posterior margin. The length, excluding spine, slightly exceeds the breadth. Details of the front are not preserved. Behind the orbital angle and above the apparent anterolateral margin formed by the outer wall of the sub-hepatic region, the true margin is represented by a short row of granules. The granules lining the hepatic margin become clustered posteriorly and the margin ends in a shallow pit. The posterolateral margin commences above the pit and its sharp, granulated edge extends almost to the posterior margin.

The regions are poorly defined. The anterior wall of the marginal pit is granulated and over the dorsal surface there is a scattering of larger granules among densely crowded minute granules. A subsurface shell layer shows a similar arrangement of pits.

DISCUSSION. *Myra trispinosa* sp. nov. is distinguishable from *M. subcarinata* by the presence of granules forming the anterolateral margin, the posterolateral margin commencing above the marginal pit, and the continued sharp edge of that margin posteriorly.

Genus *NUCIA* Dana, 1852

TYPE SPECIES. By monotypy *Nucia speciosa* Dana, 1852, from Recent of Indo-Pacific.

Figs 16, 18 *Iphiculus granulatus* sp. nov. Paratype (♂) In 61869 from Penanjong, Seria Formation, × 3. Fig. 16, dorsal view; Fig. 18, ventral view.

Fig. 17 *Iphiculus sexspinosus* sp. nov. **Holotype** In 61864 from S.5536, Seria Formation, × 2. a, dorsal view; b, ventral view.

Fig. 19 *Iphiculus sexspinosus* sp. nov. Latex cast of paratype In 61865 from S.5539, Upper Miri Formation, × 2.

Figs 20–23 *Leucosia serenei* sp. nov. from S.5548, Lower Miri Formation. Fig. 20, **holotype** In 61870, × 3. a, b dorsal and right lateral views. Fig. 21, paratype (♂) In 61871, ventral view, × 4. Fig. 22, paratype (♀) In 61872, ventral view, × 3. Fig. 23, paratype (♀) In 61873, ventral view showing the gonopores, × 3.

Fig. 24 *Leucosia tutongensis* sp. nov. **Holotype** (♂) In 61885 from S.5539, Lower Miri Formation, × 3. a, dorsal view; b, ventral view; c, right lateral view showing the gonopores.

Figs 25, 26 *Leucosia longiangulata* sp. nov. **Holotype** In 61890 from S.10474, Lower Miri Formation, × 3. Fig. 25, dorsal view; Fig. 26, right lateral view.

Fig. 27 *Myra subcarinata* sp. nov. **Holotype** In 61891 from S.5548, Lower Miri Formation, × 2. a–c, dorsal, right lateral and anterior views.



16



18



19



17a



21



22



20a



17b



23



24a



20b



25



24b



24c



27a



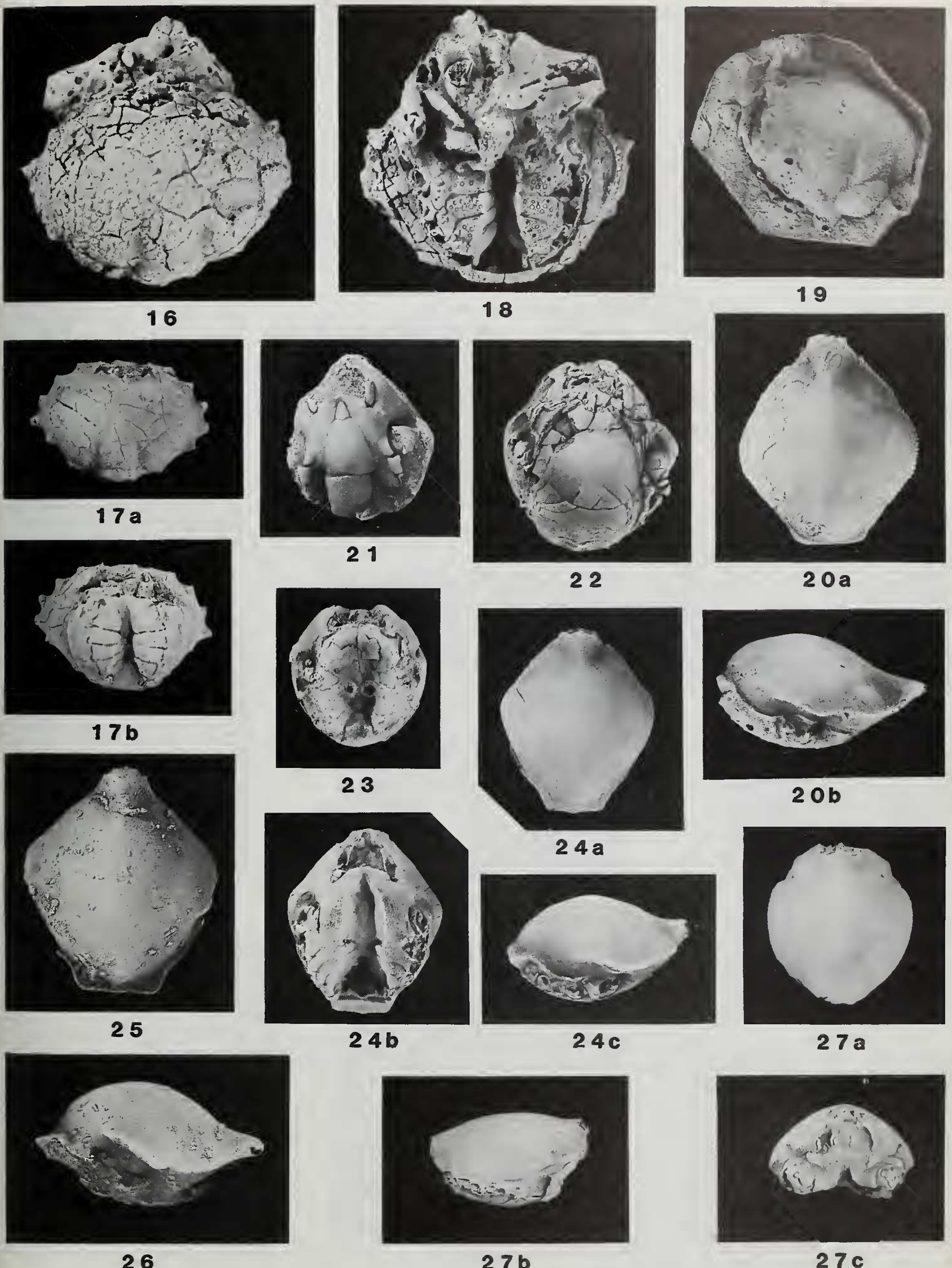
26



27b



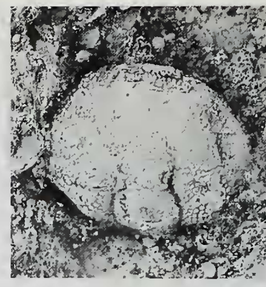
27c

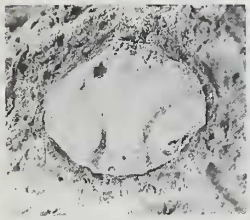

16
18
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17a
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27c


28a


28b


29


30

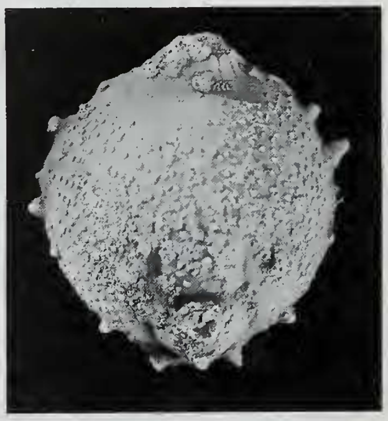

31


28c


32b


32a


33b

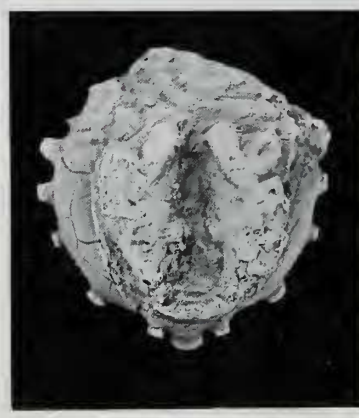

33a


32c


34a


34b

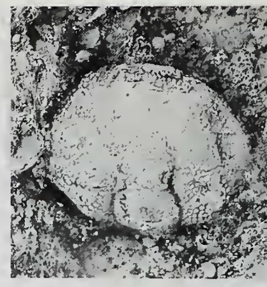

35a

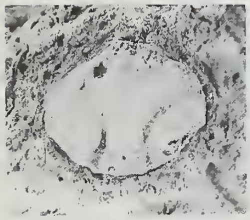

35b


28a


28b


29


30

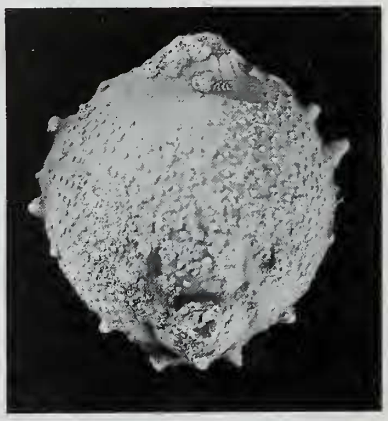

31


28c


32b


32a


33b

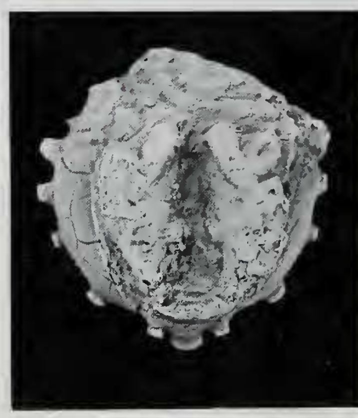

33a


32c


34a


34b


35a


35b

RANGE. Miocene to Recent.

Nucia borneoensis sp. nov. Figs 4–6

DIAGNOSIS. The carapace is subovate with a spine at the lateral angle and one on the posterolateral margin; the furrows are fully, but shallowly, developed and the dorsal surface is coarsely granulated.

NAME. 'From Borneo.'

HOLOTYPE. In 62145 (Figs 4a–c), and paratypes In 62146 (Fig. 6), In 62147 from locality S.5548; paratypes In 62148 (Figs 5a, b), In 62149 from S.10475; paratypes In 62151–6 from S.5550. All from Lower Miri Formation.

DESCRIPTION. The carapace is transverely subovate, rather more steeply arched longitudinally than transversely. There is a sharp spine at the lateral angle, another opposite the base of the cardiac region and a small one at each corner of the intestinal region. The orbitofrontal margin occupies about half the carapace width and the circular orbits are distinctly divided by a septum from ovate antennular fossae. The broadly triangular front is steeply downturned and weakly sulcate, the sulcus extending back to a postfrontal ridge. In plan view the frontal margin is nearly straight, slightly indented at the midline.

With the exception of the well-developed furrows, which are finely and evenly granulated, the dorsal surface is densely covered with coarse granules of several diameters.

The groove above the pterygostomian process is thin and smooth, the pterygostomian region itelf is elongate, granulated and just sufficiently inflated to be level with the anterolateral margin when viewed from above.

The abdominal sternites are nearly flat on either side of the deep abdominal trough; the 4th sternites are subrectangular and about twice the length of the 5th; the 6th–8th sternites diminish in size posteriorly.

DISCUSSION. See p. 20.

Nucia calculoides sp. nov. Fig. 10

DIAGNOSIS. The carapace is almost circular in outline, the anterolateral indentation is weak and the lateral spines are only feebly developed; the entire dorsal surface is covered by flattened granules.

NAME. Referring to the pebble-like surface ornament.

HOLOTYPE. In 62158 (Fig. 10) from locality S.10474, Lower Miri Formation. Paratypes In 62159–62 from S.5544, Lower Miri Formation.

DESCRIPTION. The carapace is almost circular in outline and moderately curved transversely. Longitudinally it is evenly curved after a shallow postfrontal depression. The anterolateral margins are convex to a shallow indentation at the cervical notch, then straight as far as a feeble spine, hardly bigger than the granules lining the edge of the margin. The posterolateral margins are slightly convex and there is no definite spine near the narrowly rounded posterior angle. The slightly convex posterior margin is about as wide as the orbitofrontal margin, which is rather less than half the carapace width; the front is a little produced, downturned and broadly sulcate. Viewed from above the frontal edge runs back on either side of a fine median notch dividing round the tip of the anterior mesogastric process. Fine granules line the frontal and orbital margins.

The grooves bounding the regions are thin, but sharply defined. The hepatic regions are clearly differentiated and the subcircular cardiac region is barely elevated above the general surface curvature.

Within the postfrontal depression there is a tendency for fine granules to form concave rows behind the orbits and affect the outline of the protogastric lobes. Behind, the dorsal surface is crowded with flattened granules interspersed with fine granules, and granules of varying size crowd the bottoms of the grooves. Similar granules crowd the elongate, rather subdued pterygostomian region as well as the groove above it and the branchiostegites.

Details of the ventral surface are not well preserved, but the abdominal trough extends to the tip of the 4th sternites, which are trapezoidal in outline and rather more coarsely granulate than the succeeding sternites.

DISCUSSION. See p. 20.

Nucia coxi sp. nov. Figs 30, 31

1954 *Nucia* sp. Cox *in* Collenette: 15.
1954 *Nucia* sp. (probably *N. Fennemai* Böhm): Cox *in* Collenette: 15.

DIAGNOSIS. Carapace subcircular, with three lateral spines and a spine at the posterolateral angle. Cervical groove broad but shallow, becoming almost imperceptible at the midline. Dorsal surface covered with even-sized granules.

NAME. In honour of the late Dr L.R. Cox.

HOLOTYPE. In 62164 (Fig. 30) from locality J 771, (?Lower) Miocene. Paratype In 46375 (Fig. 31) from locality NB 130, ?Lower Miocene.

DESCRIPTION. The carapace is rounded in outline, somewhat broader than long; longitudinally and transversely it is gently convex. The lateral spines are not well preserved, but basal scars indicate one on the posterolateral margin behind the marginal notch, one opposite the base of the cardiac region and another equidistant between them. The spines at the posterior angles are poorly developed. The cervical furrow is broad, but shallow as it curves gently down from the marginal notch and becomes almost imperceptible where it crosses the

Fig. 28 *Myra trispinosa* sp. nov. **Holotype** In 61893 from S.5548, Lower Miri Formation, × 1.5. a–c, dorsal, ventral and right lateral views.
Fig. 29 *Myra brevisulcata* sp. nov. **Holotype** In 61900 from S.10474, Lower Miri Formation, × 2.
Figs 30, 31 *Nucia coxi* sp. nov. Fig. 30, **holotype** In 62164 from J.771, ?Lower Miocene, × 4. Fig. 31, paratype In 46375 from NB 130, ?Lower Miocene, × 3.
Fig. 32 *Pariphiculus gselli beetsi* subsp. nov. **Holotype** In 61901 from S.5539, Lower Miri Formation, × 4. a–c, dorsal, right lateral and ventral views.
Fig. 33 *Pariphiculus papillosus* sp. nov. **Holotype** In 61902 from S.10474, Lower Miri Formation, × 3. a, b, dorsal and right lateral views.
Fig. 34 *Nucilobus symmetricus* gen. et sp. nov. **Holotype** In 61903 from S.5549, Lower Miri Formation, × 4. a, b, dorsal and right lateral views.
Fig. 35a, b *Pariphiculus verrucosus* sp. nov. **Holotype** In 61904 from S.10475, Lower Miri Formation, × 3. a, b, dorsal and ventral views. See also Fig. 35c (p. 22).

RANGE. Miocene to Recent.

Nucia borneoensis sp. nov. Figs 4–6

DIAGNOSIS. The carapace is subovate with a spine at the lateral angle and one on the posterolateral margin; the furrows are fully, but shallowly, developed and the dorsal surface is coarsely granulated.

NAME. 'From Borneo.'

HOLOTYPE. In 62145 (Figs 4a–c), and paratypes In 62146 (Fig. 6), In 62147 from locality S.5548; paratypes In 62148 (Figs 5a, b), In 62149 from S.10475; paratypes In 62151–6 from S.5550. All from Lower Miri Formation.

DESCRIPTION. The carapace is transverely subovate, rather more steeply arched longitudinally than transversely. There is a sharp spine at the lateral angle, another opposite the base of the cardiac region and a small one at each corner of the intestinal region. The orbitofrontal margin occupies about half the carapace width and the circular orbits are distinctly divided by a septum from ovate antennular fossae. The broadly triangular front is steeply downturned and weakly sulcate, the sulcus extending back to a postfrontal ridge. In plan view the frontal margin is nearly straight, slightly indented at the midline.

With the exception of the well-developed furrows, which are finely and evenly granulated, the dorsal surface is densely covered with coarse granules of several diameters.

The groove above the pterygostomian process is thin and smooth, the pterygostomian region itelf is elongate, granulated and just sufficiently inflated to be level with the anterolateral margin when viewed from above.

The abdominal sternites are nearly flat on either side of the deep abdominal trough; the 4th sternites are subrectangular and about twice the length of the 5th; the 6th–8th sternites diminish in size posteriorly.

DISCUSSION. See p. 20.

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DESCRIPTION. The carapace is almost circular in outline and moderately curved transversely. Longitudinally it is evenly curved after a shallow postfrontal depression. The anterolateral margins are convex to a shallow indentation at the cervical notch, then straight as far as a feeble spine, hardly bigger than the granules lining the edge of the margin. The posterolateral margins are slightly convex and there is no definite spine near the narrowly rounded posterior angle. The slightly convex posterior margin is about as wide as the orbitofrontal margin, which is rather less than half the carapace width; the front is a little produced, downturned and broadly sulcate. Viewed from above the frontal edge runs back on either side of a fine median notch dividing round the tip of the anterior mesogastric process. Fine granules line the frontal and orbital margins.

The grooves bounding the regions are thin, but sharply defined. The hepatic regions are clearly differentiated and the subcircular cardiac region is barely elevated above the general surface curvature.

Within the postfrontal depression there is a tendency for fine granules to form concave rows behind the orbits and affect the outline of the protogastric lobes. Behind, the dorsal surface is crowded with flattened granules interspersed with fine granules, and granules of varying size crowd the bottoms of the grooves. Similar granules crowd the elongate, rather subdued pterygostomian region as well as the groove above it and the branchiostegites.

Details of the ventral surface are not well preserved, but the abdominal trough extends to the tip of the 4th sternites, which are trapezoidal in outline and rather more coarsely granulate than the succeeding sternites.

DISCUSSION. See p. 20.

Nucia coxi sp. nov. Figs 30, 31

1954 *Nucia* sp. Cox *in* Collenette: 15.
1954 *Nucia* sp. (probably *N. Fennemai* Böhm): Cox *in* Collenette: 15.

DIAGNOSIS. Carapace subcircular, with three lateral spines and a spine at the posterolateral angle. Cervical groove broad but shallow, becoming almost imperceptible at the midline. Dorsal surface covered with even-sized granules.

NAME. In honour of the late Dr L.R. Cox.

HOLOTYPE. In 62164 (Fig. 30) from locality J 771, (?Lower) Miocene. Paratype In 46375 (Fig. 31) from locality NB 130, ?Lower Miocene.

DESCRIPTION. The carapace is rounded in outline, somewhat broader than long; longitudinally and transversely it is gently convex. The lateral spines are not well preserved, but basal scars indicate one on the posterolateral margin behind the marginal notch, one opposite the base of the cardiac region and another equidistant between them. The spines at the posterior angles are poorly developed. The cervical furrow is broad, but shallow as it curves gently down from the marginal notch and becomes almost imperceptible where it crosses the

Fig. 28 *Myra trispinosa* sp. nov. **Holotype** In 61893 from S.5548, Lower Miri Formation, × 1.5. a–c, dorsal, ventral and right lateral views.
Fig. 29 *Myra brevisulcata* sp. nov. **Holotype** In 61900 from S.10474, Lower Miri Formation, × 2.
Figs 30, 31 *Nucia coxi* sp. nov. Fig. 30, **holotype** In 62164 from J.771, ?Lower Miocene, × 4. Fig. 31, paratype In 46375 from NB 130, ?Lower Miocene, × 3.
Fig. 32 *Pariphiculus gselli beetsi* subsp. nov. **Holotype** In 61901 from S.5539, Lower Miri Formation, × 4. a–c, dorsal, right lateral and ventral views.
Fig. 33 *Pariphiculus papillosus* sp. nov. **Holotype** In 61902 from S.10474, Lower Miri Formation, × 3. a, b, dorsal and right lateral views.
Fig. 34 *Nucilobus symmetricus* gen. et sp. nov. **Holotype** In 61903 from S.5549, Lower Miri Formation, × 4. a, b, dorsal and right lateral views.
Fig. 35a, b *Pariphiculus verrucosus* sp. nov. **Holotype** In 61904 from S.10475, Lower Miri Formation, × 3. a, b, dorsal and ventral views. See also Fig. 35c (p. 22).

midline; it is joined by fine, very short, straight hepatic furrows. On each protogastric lobe an obscure ridge (more noticeable on an internal mould) runs parallel to the cervical furrow amd has a node at the posterior end; similar-sized nodes occur close to the midline on the urogastric lobe. Deep furrows separate the urogastric lobe and cardiac region from one another and from the branchial regions. The tumid, rounded-pentagonal cardiac region does not overhang the posterior margin; a narrow median tongue extends into the urogastric lobe. The dorsal surface is densely crowded with more or less even-sized granules.

Discussion of species of *Nucia*. There is a noticeable difference in the length/width ratios between *N. borneoensis* and *N. calculoides*, the latter being rather wider in relation to length. It differs also in having the cardiac region wider than the base of the mesogastric lobe and ovate rather than rounded as in *N. borneoensis*; the primary granules on *N. borneoensis* are more widely dispersed and hemispherical rather than being densely packed and flattened as they are in *N. calculoides*.

The weak lateral extension of the cervical furrow and hepatic furrows, together with the finer, denser granulation, distinguishes *N. coxi* from the foregoing species. *N. baripadensis* Bachmayer & Mohanti, 1973 (Miocene, eastern India) is rather similar in outline to *N. coxi* but has a sharper indentation in the anterolateral margin; the anterior portions of the furrows are as weakly developed and the cardiac region of the Indian species appears to be more ovate; its surface ornament consists of numerous cratered pits – possibly the ornament of a sub-surface shell layer.

Of Recent species, the type species *N. speciosa* differs in having a rather more protruding front and areolated lobes which obscure the lateral extension of the cervical and hepatic furrows, but it has well-defined median gastric and cardiac lobes in common with *N. borneoensis* and *N. calculoides*. *Nucia tuberculosa* Milne Edwards, 1874 and *Nucia perlata* Sakai, 1965 have a rounded carapace with subdued marginal spines; the latter has well-defined hepatic and frontal lobes.

Nucia fennemai Böhm, 1922, from the ?Lower Miocene of Java (l/w = 0.8) is relatively broader than *N. coxi*, which has a l/w ratio of 0.9. Otherwise they are very similar; they each have three lateral spines and a posterolateral spine. *N. coxi* differs in that it has a wider front, the cervical groove is more strongly impressed and the dorsal surface is covered with densely crowded even-sized granules. The granules on the dorsal surface of *N. fennemai* are not so dense and become much more widely spaced on the branchial regions. *N. fennemai* is relatively narrower than both *N. borneoensis* (l/w = 0.75) and *N. calculoides* (l/w = 0.65). Both *N. borneoensis* and *N. calculoides* have much coarser ornament and that of *N. calculoides* is pebble-like.

Genus *NUCILOBUS* nov.

Type species. *Nucilobus symmetricus* sp. nov.

Diagnosis. Carapace longer than broad, subovate with five small marginal tubercles. The cervical furrow is shallow medially, but has deep anterolateral extensions to the margin; it is continuous with a furrow delimiting the urogastric and cardiac regions. Hepatic furrows present. The dorsal surface has a tubercular ornamentation and there are three pairs of pits in the cervical/urocardiac furrows.

Name. Varied from *Nucia*. Masculine.

Nucilobus symmetricus gen. et sp. nov. Fig. 34

Diagnosis. As for genus.

Name. 'Symmetrical', from the bilateral arrangement of the surface ornament.

Holotype. A female, In 61903 (Figs 34a, b) from locality S.5549, Lower Miri Formation.

Description. The carapace is subovate in outline, a little longer than wide and widest at about midlength. The anterolateral margins are slightly constricted, both behind the orbits and before the cervical notch; they are short and lined with 4 or 5 granules. Behind the cervical notch a very small tubercle is followed by four evenly-spaced larger ones; the fourth, set opposite the cardiac region, is followed by another one at the posterior angle. The orbitofrontal margin occupies half the carapace width. It is not produced and is directed almost straight forward; viewed from the side the curvature is only a little less than the general longitudinal curvature of the carapace. The front is wide, steeply downturned into an acutely triangular rostrum, and a deep median sulcus bifurcates, with each branch partially encircling a 'frontal lobe'.

The cervical furrow is deep from the lateral margin to the outer angle of the mesogastric lobe, but becomes very faint where it crosses the midline; anteriorly weak furrows partly separate the hepatic regions from the protogastric lobes. Deep grooves separate the rather large subquadrate urogastric lobe from the cardiac region and the cardiac from the intestinal and branchial regions. The tumid, rounded-pentagonal cardiac region does not overhang the posterior margin and is about as wide as the intestinal region, on which the corner tubercles are somewhat more spiny than the marginal ones.

There is a pit at the junction of the cervical and hepatic furrows, one at the outer angle of the urogastric and another midway along that lobe. A row of four granules lining the anterior border of the urogastric lobe is followed by six granules encircling a median one. Granules forming an outer ring on the cardiac region enclose two larger ones and the remaining surface is sparsely ornamented by granules of several diameters bilaterally distributed in semicircular or linear patterns.

The pterygostomian region is very narrow and lined with granules extending beyond the anterolateral margin.

Discussion. In having anterolaterally developed cervical furrows and hepatic furrows *Nucilobus symmetricus* has elements in common with *Nucia* – particularly the new forms *N. borneoensis* (p. 19) and *N. calculoides* (p. 19) described above. The new genus differs from *Nucia*, however, in being much longer than broad and in the presence of the furrow pits (although *Nucia speciosa* appears to have two pairs: one at the broadest part of the mesogastric lobe and one midlength of urogastric lobe). *Pariphiculus* (p. 21) has a similarly elongate carapace, but lacks the prominent grooves. This suggests a lineage from *Nucilobus* to *Pariphiculus* through a reduction in carapace grooves, especially the cervical groove which in *Pariphiculus* is seen only as an anterolateral notch.

midline; it is joined by fine, very short, straight hepatic furrows. On each protogastric lobe an obscure ridge (more noticeable on an internal mould) runs parallel to the cervical furrow amd has a node at the posterior end; similar-sized nodes occur close to the midline on the urogastric lobe. Deep furrows separate the urogastric lobe and cardiac region from one another and from the branchial regions. The tumid, rounded-pentagonal cardiac region does not overhang the posterior margin; a narrow median tongue extends into the urogastric lobe. The dorsal surface is densely crowded with more or less even-sized granules.

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Genus ***NUCILOBUS*** nov.

Type species. *Nucilobus symmetricus* sp. nov.

Diagnosis. Carapace longer than broad, subovate with five small marginal tubercles. The cervical furrow is shallow medially, but has deep anterolateral extensions to the margin; it is continuous with a furrow delimiting the urogastric and cardiac regions. Hepatic furrows present. The dorsal surface has a tubercular ornamentation and there are three pairs of pits in the cervical/urocardiac furrows.

Name. Varied from *Nucia*. Masculine.

Nucilobus symmetricus gen. et sp. nov. Fig. 34

Diagnosis. As for genus.

Name. 'Symmetrical', from the bilateral arrangement of the surface ornament.

Holotype. A female, In 61903 (Figs 34a, b) from locality S.5549, Lower Miri Formation.

Description. The carapace is subovate in outline, a little longer than wide and widest at about midlength. The anterolateral margins are slightly constricted, both behind the orbits and before the cervical notch; they are short and lined with 4 or 5 granules. Behind the cervical notch a very small tubercle is followed by four evenly-spaced larger ones; the fourth, set opposite the cardiac region, is followed by another one at the posterior angle. The orbitofrontal margin occupies half the carapace width. It is not produced and is directed almost straight forward; viewed from the side the curvature is only a little less than the general longitudinal curvature of the carapace. The front is wide, steeply downturned into an acutely triangular rostrum, and a deep median sulcus bifurcates, with each branch partially encircling a 'frontal lobe'.

The cervical furrow is deep from the lateral margin to the outer angle of the mesogastric lobe, but becomes very faint where it crosses the midline; anteriorly weak furrows partly separate the hepatic regions from the protogastric lobes. Deep grooves separate the rather large subquadrate urogastric lobe from the cardiac region and the cardiac from the intestinal and branchial regions. The tumid, rounded-pentagonal cardiac region does not overhang the posterior margin and is about as wide as the intestinal region, on which the corner tubercles are somewhat more spiny than the marginal ones.

There is a pit at the junction of the cervical and hepatic furrows, one at the outer angle of the urogastric and another midway along that lobe. A row of four granules lining the anterior border of the urogastric lobe is followed by six granules encircling a median one. Granules forming an outer ring on the cardiac region enclose two larger ones and the remaining surface is sparsely ornamented by granules of several diameters bilaterally distributed in semicircular or linear patterns.

The pterygostomian region is very narrow and lined with granules extending beyond the anterolateral margin.

Discussion. In having anterolaterally developed cervical furrows and hepatic furrows *Nucilobus symmetricus* has elements in common with *Nucia* – particularly the new forms *N. borneoensis* (p. 19) and *N. calculoides* (p. 19) described above. The new genus differs from *Nucia*, however, in being much longer than broad and in the presence of the furrow pits (although *Nucia speciosa* appears to have two pairs: one at the broadest part of the mesogastric lobe and one midlength of urogastric lobe). *Pariphiculus* (p. 21) has a similarly elongate carapace, but lacks the prominent grooves. This suggests a lineage from *Nucilobus* to *Pariphiculus* through a reduction in carapace grooves, especially the cervical groove which in *Pariphiculus* is seen only as an anterolateral notch.

Genus *PARIPHICULUS* Alcock, 1896

TYPE SPECIES. By subsequent designation of Rathbun, 1922: *Randallia coronata* Alcock & Anderson, 1894 [ICZN Opinion 73]; from Recent of the Bay of Bengal.

RANGE. Middle Miocene to Recent.

Pariphiculus gselli Beets *beetsi* ssp. nov. Fig. 32

DIAGNOSIS. Narrow (*trans.*) intestinal region with extra tubercle at the posterolateral limit of the metabranchial region. Cardiac tubercles and pair of tubercles parallel to the branchiocardic groove obsolete.

NAME. In honour of Dr C. Beets.

HOLOTYPE. In 61901 (Figs 32a–c) from locality S.5539, Lower Miri Formation.

DESCRIPTION. The carapace is small, subglobose and subcircular in outline; the length slightly exceeds the breadth. Of the four tubercular processes on the anterolateral margin, the 1st and 2nd are hardly more than enlargements of the granules forming the surface ornament; the 4th, the largest, occurs at the widest part of the carapace and is followed immediately by another tubercle and one, much reduced, lies opposite the cardiac region. The orbitofrontal margin, occupying about a third of the carapace width, is only a little produced and barely upturned; the very small, acutely triangular rostrum is sharply downturned and a low, sinuous ridge borders the frontal margin.

The basal portion of the mesogastric region is defined by faint furrows which rapidly deepen posteriorly and delimit the urogastric and cardiac regions. The bulbous, almost circular cardiac region overhangs the posterior margin; it has two obscure, even-sized granules in line medially and is wider than the short intestinal region on which the corner tubercles are similar to the larger-sized lateral ones.

A narrow postfrontal area is only sparsely granulated, but the remainder of the dorsal surface is densely and finely granulated, the granules becoming a little coarser towards the metabranchial lobes. A row of granules, becoming sparser and finer posteriorly, borders the pleural suture. The pterygostomian region is weakly tumid and granulated; when viewed from above, a small tubercle at its centre is clearly visible beyond the lateral margin.

The abdominal sternites are shallowly depressed, more or less rectangular in outline and decrease in size posteriorly.

DISCUSSION. The new subspecies differs from the nominal subspecies (Beets 1950) from the Rembangian (Tf_2) of Java only by the absence of the pair of tubercles on the metabranchial region parallel to the cervical groove and the absence of the single tubercle on the urogastric region. It also differs from *Pariphiculus coronatus* (Alcock & Anderson, 1894) from the Recent of the Bay of Bengal by the absence of the same tubercles, but *P. gselli beetsi* subsp. nov. is relatively wider. *Pariphiculus rostratus* Alcock, 1896 from the Recent of the Malabar Coast differs from *P. g. beetsi* because in *P. rostratus* the cardiac tubercles have become extended into spines.

Pariphiculus papillosus sp. nov. Fig. 33

DIAGNOSIS. The carapace is subovate, slightly longer than broad, with six small marginal tubercles; the larger, hindmost tubercle on the cardiac region barely overlaps the posterior margin; the dorsal surface is densely granulated.

NAME. From the papillate nature of the marginal spines.

HOLOTYPE. In 61902 (Figs 33a, b) from locality S.10474, Lower Miri Formation.

DESCRIPTION. The carapace is subglobose and subovate in outline, only a little longer than broad with the greatest width occurring at about midlength. On the anterolateral margins are four small, nipple-like tubercles of which the first is much reduced in size; of two similar tubercles on the posterolateral margins, the first is very small and the second lies opposite the hinder, larger tubercle on the cardiac region. The posterior margin is about as wide as the frontal border. The orbitofrontal margin is directed a little upwards; the front takes up the middle third and the slightly produced, acutely triangular rostrum is downturned at its tip. The upper orbital margin is thin and deeply pierced by two notches.

Apart from the furrows delineating the basal part of the urogastric lobe and cardiac region, the lobes are undifferentiated. The bulbous, almost circular cardiac region has two tubercles, the hindmost of which barely overlaps the posterior margin. The short intestinal is as wide as the cardiac and the spine above each corner is finer and more attenuated than those on the lateral margins. There is a small tubercle on each metabranchial lobe close to the intestinal lobe.

With the exception of a narrow postfrontal area and a narrow strip above the 2nd–4th lateral tubercles, the dorsal surface is covered with densely crowded granules of more or less even size.

The lateral edges are rounded and the pterygostomian region is sparsely granulated.

DISCUSSION. This species differs from all other *Pariphiculus* by the papillate nature of the marginal spines.

Pariphiculus verrucosus sp. nov. Fig. 35

DIAGNOSIS. The carapace is broadly ovate with four warty tubercles on the lateral margins; the dorsal surface is granulated and has seven tubercles, of which the hindmost one on the cardiac region clearly overhangs the posterior margin.

NAME. 'Warty', from the appearance of the tubercles.

HOLOTYPE. In 61904 (Figs 35a–c) from locality S.10475, Lower Miri Formation.

DESCRIPTION. The carapace is similar in outline to the previous species but widest at the anterior third. There are several granules decreasing in size on the short, convex anterolateral margins; a longer, warty tubercle occurs immediately after an obscure cervical notch, and is followed on the convex posterolateral margin by three other tubercles of which the second is somewhat smaller.

The orbitofrontal margin is damaged in the holotype, but appears to have been only a little upturned. The urogastric lobe and the cardiac and intestinal regions are separated from one another and from the branchial regions by deep grooves. When viewed from the side the subpentagonal cardiac, and to a lesser extent the narrow, bar-like intestinal regions, overlap the posterior margin. The bottoms of the furrows are smooth and except for the cardiac and intestinal regions, which are minutely granulated, the dorsal surface is crowded with coarse granules of several diameters. There are, in addition,

Genus *PARIPHICULUS* Alcock, 1896

TYPE SPECIES. By subsequent designation of Rathbun, 1922: *Randallia coronata* Alcock & Anderson, 1894 [ICZN Opinion 73]; from Recent of the Bay of Bengal.

RANGE. Middle Miocene to Recent.

Pariphiculus gselli Beets ***beetsi*** ssp. nov. Fig. 32

DIAGNOSIS. Narrow (*trans.*) intestinal region with extra tubercle at the posterolateral limit of the metabranchial region. Cardiac tubercles and pair of tubercles parallel to the branchiocardic groove obsolete.

NAME. In honour of Dr C. Beets.

HOLOTYPE. In 61901 (Figs 32a–c) from locality S.5539, Lower Miri Formation.

DESCRIPTION. The carapace is small, subglobose and subcircular in outline; the length slightly exceeds the breadth. Of the four tubercular processes on the anterolateral margin, the 1st and 2nd are hardly more than enlargements of the granules forming the surface ornament; the 4th, the largest, occurs at the widest part of the carapace and is followed immediately by another tubercle and one, much reduced, lies opposite the cardiac region. The orbitofrontal margin, occupying about a third of the carapace width, is only a little produced and barely upturned; the very small, acutely triangular rostrum is sharply downturned and a low, sinuous ridge borders the frontal margin.

The basal portion of the mesogastric region is defined by faint furrows which rapidly deepen posteriorly and delimit the urogastric and cardiac regions. The bulbous, almost circular cardiac region overhangs the posterior margin; it has two obscure, even-sized granules in line medially and is wider than the short intestinal region on which the corner tubercles are similar to the larger-sized lateral ones.

A narrow postfrontal area is only sparsely granulated, but the remainder of the dorsal surface is densely and finely granulated, the granules becoming a little coarser towards the metabranchial lobes. A row of granules, becoming sparser and finer posteriorly, borders the pleural suture. The pterygostomian region is weakly tumid and granulated; when viewed from above, a small tubercle at its centre is clearly visible beyond the lateral margin.

The abdominal sternites are shallowly depressed, more or less rectangular in outline and decrease in size posteriorly.

DISCUSSION. The new subspecies differs from the nominal subspecies (Beets 1950) from the Rembangian (Tf_2) of Java only by the absence of the pair of tubercles on the metabranchial region parallel to the cervical groove and the absence of the single tubercle on the urogastric region. It also differs from *Pariphiculus coronatus* (Alcock & Anderson, 1894) from the Recent of the Bay of Bengal by the absence of the same tubercles, but *P. gselli beetsi* subsp. nov. is relatively wider. *Pariphiculus rostratus* Alcock, 1896 from the Recent of the Malabar Coast differs from *P. g. beetsi* because in *P. rostratus* the cardiac tubercles have become extended into spines.

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DIAGNOSIS. The carapace is subovate, slightly longer than broad, with six small marginal tubercles; the larger, hindmost tubercle on the cardiac region barely overlaps the posterior margin; the dorsal surface is densely granulated.

NAME. From the papillate nature of the marginal spines.

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Apart from the furrows delineating the basal part of the urogastric lobe and cardiac region, the lobes are undifferentiated. The bulbous, almost circular cardiac region has two tubercles, the hindmost of which barely overlaps the posterior margin. The short intestinal is as wide as the cardiac and the spine above each corner is finer and more attenuated than those on the lateral margins. There is a small tubercle on each metabranchial lobe close to the intestinal lobe.

With the exception of a narrow postfrontal area and a narrow strip above the 2nd–4th lateral tubercles, the dorsal surface is covered with densely crowded granules of more or less even size.

The lateral edges are rounded and the pterygostomian region is sparsely granulated.

DISCUSSION. This species differs from all other *Pariphiculus* by the papillate nature of the marginal spines.

Pariphiculus verrucosus sp. nov. Fig. 35

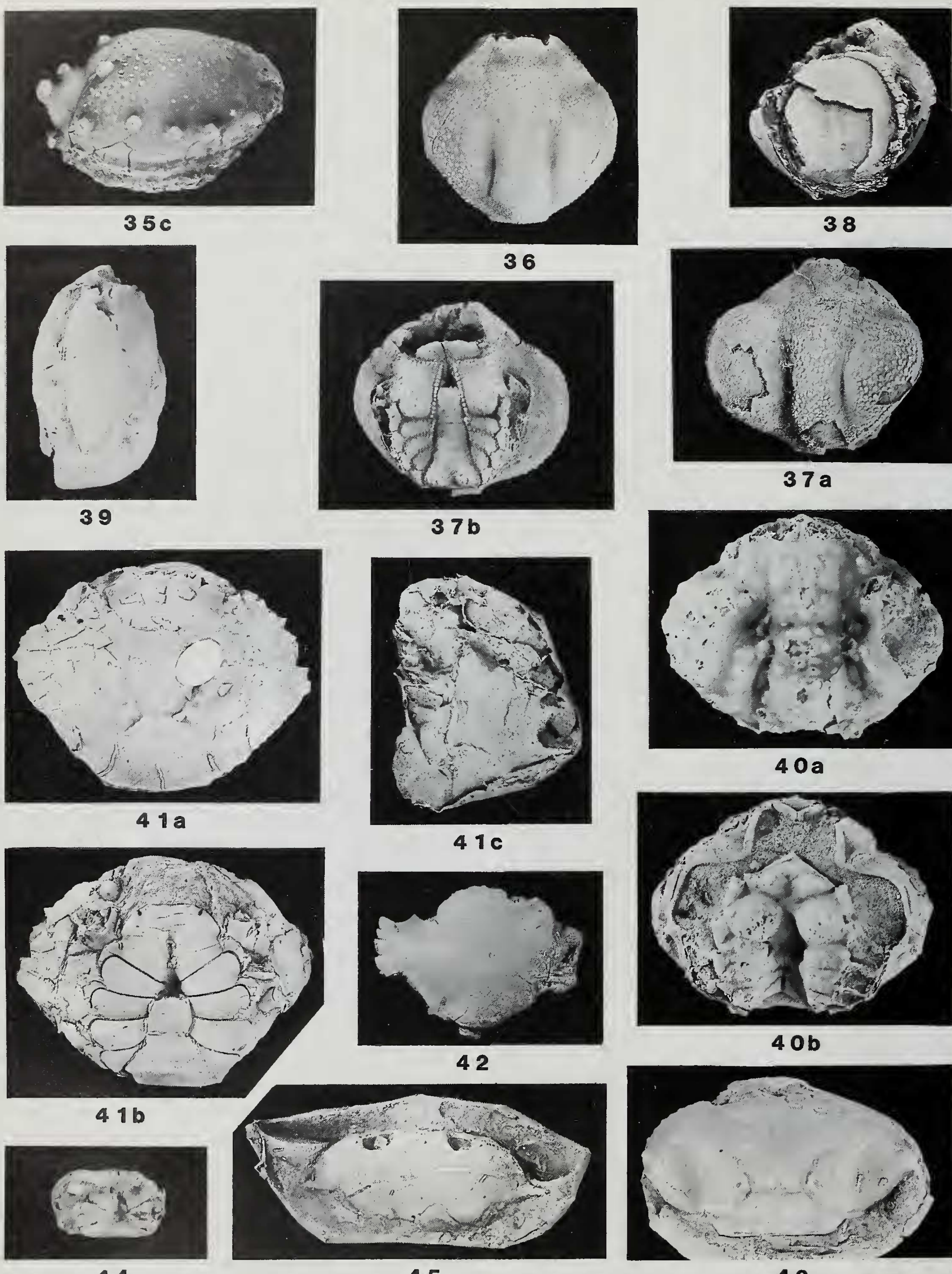
DIAGNOSIS. The carapace is broadly ovate with four warty tubercles on the lateral margins; the dorsal surface is granulated and has seven tubercles, of which the hindmost one on the cardiac region clearly overhangs the posterior margin.

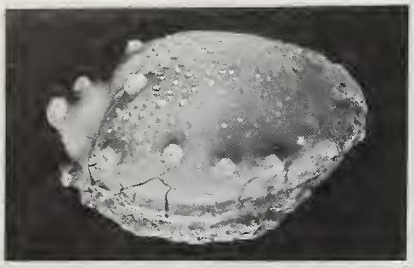
NAME. 'Warty', from the appearance of the tubercles.

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DESCRIPTION. The carapace is similar in outline to the previous species but widest at the anterior third. There are several granules decreasing in size on the short, convex anterolateral margins; a longer, warty tubercle occurs immediately after an obscure cervical notch, and is followed on the convex posterolateral margin by three other tubercles of which the second is somewhat smaller.

The orbitofrontal margin is damaged in the holotype, but appears to have been only a little upturned. The urogastric lobe and the cardiac and intestinal regions are separated from one another and from the branchial regions by deep grooves. When viewed from the side the subpentagonal cardiac, and to a lesser extent the narrow, bar-like intestinal regions, overlap the posterior margin. The bottoms of the furrows are smooth and except for the cardiac and intestinal regions, which are minutely granulated, the dorsal surface is crowded with coarse granules of several diameters. There are, in addition,


35c
36
38
39
37b
37a
41a
41c
40a
41b
42
40b
44
45
43


35c


36


38


39

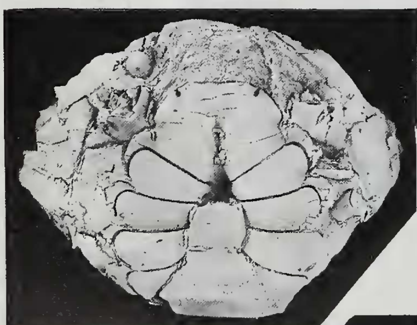

37b


37a


41a


41c


40a


41b


42


40b


44


45


43

seven warty tubercles: one on the urogastric lobe; two, the foremost of which is smaller, on the cardiac region; one on each metabranchial lobe; and one at each corner of the intestinal region.

The sides are inclined a little inwards and the slightly tumid pterygostomian region has a tubercle clearly visible when viewed from above.

DISCUSSION. In the wart-like marginal and dorsal tubercles *P. verrucosus* has a marked affinity to *Pariphiculus agariciferus* Ihle, 1918, a Recent species from Roti Island (type locality) near Timor and Japan, but the latter species has additional tubercles on the gastric region, a much coarser surface granulation and poorly-defined grooves delimiting the regions.

Genus *PHILYRA* Leach, 1817

TYPE SPECIES. By subsequent designation of H. Milne Edwards, 1837: *Cancer globus* Fabricius, 1775 [ICZN Opinion 712]; from Recent of West Africa.

RANGE. Pliocene to Recent.

Philyra granulosa sp. nov. Figs 36–38

DIAGNOSIS. Carapace octagonal with an entire lateral margin, post-frontal depression shallow; dorsal surface densely granulated.

NAME. 'Granulated'.

HOLOTYPE. In 61905 (Fig. 36), and paratypes In 61906 (Figs 37a, b), In 61907 (Fig. 38), In 61908–10 from locality S.5548, Lower Miri Formation. Paratypes In 61911–2 from S.5538, Upper Miri Formation; In 61913–4 from S.5549, Lower Miri Formation.

DESCRIPTION. The subpyriform carapace is a little longer than wide; in side view the front is a little upturned with a shallow postfrontal depression. The anterolateral margins are short, straight to slightly convex, and the beaded edge surrounding the margin is not interrupted where the lateral extension of the cervical furrow reaches the edge. The posterior margin is as wide as the orbitofrontal margin, which occupies about half the carapace width. The front is wide, triangular, steeply downturned and broadly sulcate above. The orbits are directed slightly upwards and of the two fine fissures in the upper margins, the outermost lies close to the beaded edge.

Broad furrows separate the median gastric from the branchial regions and there is a small median incursion of the straight-sided cardiac region into the urogastric lobe; the rounded base of the cardiac region is confluent with a small, circular intestinal region. The hepatic regions are weakly tumid; deep subhepatic regions are inclined almost at right angles to the margin, and an almost smooth, flattened upper part is divided from a narrow, tumid lower part by a line of granules diverging from the marginal ones.

Numerous granules crowd the dorsal surface, although in some specimens the postfrontal depression is almost smooth; there is a denser, finer mass on either side of the cardiac region and a tendency for those on the branchial region to become coarser laterally.

In the male the 1st and 2nd sternites form a narrow triangular strip steeply inclined into the body cavity anteriorly and posteriorly sending back a narrow tongue separating the 3rd sternites. The 3rd sternites are subrectangular with a sinuous anterior border and a contra-sinuous posterior border; the subrectangular 4th sternites are wider than the 3rd and longer than the 5th–7th sternites, which become smaller and progressively more chordate posteriorly. The 4th sternites are granulated; the other sternites are relatively smooth and the abdominal trough is lined with beaded granules.

On specimen In 61906 (Figs 37a, b), a large bopyriform swelling occupies the entire left-hand branchial region.

DISCUSSION. The evenly rounded transverse section and coarsely granulated dorsal surface most readily distinguish this species; *Philyra adamsii* Bell, 1855 has granules restricted to the posterior half of the carapace, while *P. pisum* de Haan, 1841, *P. carinata* Bell, 1855 and *P. kanekoi* Sakai, 1934, all have regionally distributed granules and all have a weak median carina.

Genus *TYPILOBUS* Stoliczka, 1871

TYPE SPECIES. By monotypy *Typilobus granulosus* Stoliczka, 1871 from the Lower Miocene of Sind, India.

RANGE. Middle Eocene to Middle Miocene.

Typilobus marginatus sp. nov. Fig. 7

DIAGNOSIS. A large, transversely ovate carapace with very thin and granulated anterolateral edge.

Fig. 35c *Pariphiculus verrucosus* sp. nov. Right lateral view of **holotype** In 61904 from S.10475, Lower Miri Formation, × 3. See also Figs 35a, b (p. 18).
Figs 36–38 *Philyra granulosa* sp. nov. From S.5548, Lower Miri Formation, × 4. Fig. 36, dorsal view of **holotype** In 61905. Fig. 37, paratype (♂) In 61906. a, b, dorsal and ventral views of male with bopyriform swelling of left branchial chamber. Fig. 38, ventral view of paratype (♀) In 61907.
Fig. 39 *Raninoides* sp. In 61915 from S.5539, Lower Miri Formation, × 2.
Fig. 40 *Parthenope (Rhinolambrus) sublitoralis* sp. nov. **Holotype** In 61917 from S.5548, Lower Miri Formation, × 3. a, b, dorsal and ventral views.
Figs 41, 42 *Charybdis (Charybdis) feriata* (Linn.) *bruneiensis* subsp. nov. from S.4965, ?late Middle Pleistocene. Fig. 41, **holotype** In 59015. a, b, dorsal and ventral views, ×1; c, latex cast from external mould to show anterolateral spines, × 2. Fig. 42, dorsal view of paratype In 59012 from S.4918, ?late Middle Pleistocene, × 2.
Figs 43–45 *Portunus obvallatus* sp. nov. from S.5539, Upper Miri Formation. Fig. 43, dorsal view of **holotype** In 61947, × 3. Fig. 44, ventral view of paratype In 61948, × 2. Fig. 45, latex cast from external mould of paratype In 61949, × 3.

seven warty tubercles: one on the urogastric lobe; two, the foremost of which is smaller, on the cardiac region; one on each metabranchial lobe; and one at each corner of the intestinal region.

The sides are inclined a little inwards and the slightly tumid pterygostomian region has a tubercle clearly visible when viewed from above.

DISCUSSION. In the wart-like marginal and dorsal tubercles *P. verrucosus* has a marked affinity to *Pariphiculus agariciferus* Ihle, 1918, a Recent species from Roti Island (type locality) near Timor and Japan, but the latter species has additional tubercles on the gastric region, a much coarser surface granulation and poorly-defined grooves delimiting the regions.

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RANGE. Pliocene to Recent.

Philyra granulosa sp. nov. Figs 36–38

DIAGNOSIS. Carapace octagonal with an entire lateral margin, post-frontal depression shallow; dorsal surface densely granulated.

NAME. 'Granulated'.

HOLOTYPE. In 61905 (Fig. 36), and paratypes In 61906 (Figs 37a, b), In 61907 (Fig. 38), In 61908–10 from locality S.5548, Lower Miri Formation. Paratypes In 61911–2 from S.5538, Upper Miri Formation; In 61913–4 from S.5549, Lower Miri Formation.

DESCRIPTION. The subpyriform carapace is a little longer than wide; in side view the front is a little upturned with a shallow postfrontal depression. The anterolateral margins are short, straight to slightly convex, and the beaded edge surrounding the margin is not interrupted where the lateral extension of the cervical furrow reaches the edge. The posterior margin is as wide as the orbitofrontal margin, which occupies about half the carapace width. The front is wide, triangular, steeply downturned and broadly sulcate above. The orbits are directed slightly upwards and of the two fine fissures in the upper margins, the outermost lies close to the beaded edge.

Broad furrows separate the median gastric from the branchial regions and there is a small median incursion of the straight-sided cardiac region into the urogastric lobe; the rounded base of the cardiac region is confluent with a small, circular intestinal region. The hepatic regions are weakly tumid; deep subhepatic regions are inclined almost at right angles to the margin, and an almost smooth, flattened upper part is divided from a narrow, tumid lower part by a line of granules diverging from the marginal ones.

Numerous granules crowd the dorsal surface, although in some specimens the postfrontal depression is almost smooth; there is a denser, finer mass on either side of the cardiac region and a tendency for those on the branchial region to become coarser laterally.

In the male the 1st and 2nd sternites form a narrow triangular strip steeply inclined into the body cavity anteriorly and posteriorly sending back a narrow tongue separating the 3rd sternites. The 3rd sternites are subrectangular with a sinuous anterior border and a contra-sinuous posterior border; the subrectangular 4th sternites are wider than the 3rd and longer than the 5th–7th sternites, which become smaller and progressively more chordate posteriorly. The 4th sternites are granulated; the other sternites are relatively smooth and the abdominal trough is lined with beaded granules.

On specimen In 61906 (Figs 37a, b), a large bopyriform swelling occupies the entire left-hand branchial region.

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Genus *TYPILOBUS* Stoliczka, 1871

TYPE SPECIES. By monotypy *Typilobus granulosus* Stoliczka, 1871 from the Lower Miocene of Sind, India.

RANGE. Middle Eocene to Middle Miocene.

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DIAGNOSIS. A large, transversely ovate carapace with very thin and granulated anterolateral edge.

Fig. 35c *Pariphiculus verrucosus* sp. nov. Right lateral view of **holotype** In 61904 from S.10475, Lower Miri Formation, × 3. See also Figs 35a, b (p. 18).

Figs 36–38 *Philyra granulosa* sp. nov. From S.5548, Lower Miri Formation, × 4. Fig. 36, dorsal view of **holotype** In 61905. Fig. 37, paratype (♂) In 61906. a, b, dorsal and ventral views of male with bopyriform swelling of left branchial chamber. Fig. 38, ventral view of paratype (♀) In 61907.

Fig. 39 *Raninoides* sp. In 61915 from S.5539, Lower Miri Formation, × 2.

Fig. 40 *Parthenope (Rhinolambrus) sublitoralis* sp. nov. **Holotype** In 61917 from S.5548, Lower Miri Formation, × 3. a, b, dorsal and ventral views.

Figs 41, 42 *Charybdis (Charybdis) feriata* (Linn.) *bruneiensis* subsp. nov. from S.4965, ?late Middle Pleistocene. Fig. 41, **holotype** In 59015. a, b, dorsal and ventral views, ×1; c, latex cast from external mould to show anterolateral spines, × 2. Fig. 42, dorsal view of paratype In 59012 from S.4918, ?late Middle Pleistocene, × 2.

Figs 43–45 *Portunus obvallatus* sp. nov. from S.5539, Upper Miri Formation. Fig. 43, dorsal view of **holotype** In 61947, × 3. Fig. 44, ventral view of paratype In 61948, × 2. Fig. 45, latex cast from external mould of paratype In 61949, × 3.

NAME. Referring to the sharp lateral margin.

HOLOTYPE. In 62163 (Figs 7a–d) from locality NB 11541, Tungku Formation, Middle Miocene.

DESCRIPTION. The length of the transversely oval carapace is about four-fifths of the breadth measured immediately in front of the lateral spines; it is moderately arched transversely and longitudinally flatly arched behind a weak postfrontal depression. The anterolateral margins are convex with hardly any indentation at the cervical notch. The spine at the lateral angle is set a little behind the mid-carapace length. It is bluntly rounded and upturned, and anteriorly it tapers into a very thin edge lined with granules. At the cervical notch the ridge divides; the stronger, lower branch is interrupted by a large cluster of granules on the pterygostomian region and terminates in a small tubercle beneath the orbit, while the upper branch continues to the upper orbital margin. The posterolateral margins are nearly straight with a small, wart-like tubercle opposite the widest part of the cardiac region. A similar tubercle occurs at the posterior angle and the posterior margin is about as wide as the orbitofrontal margin. The orbitofrontal margin occupies a third of the carapace width and the sides of the barely projecting front are feebly inclined to a shallow median depression. The frontal edge is lined with two or three rows of fine granules, giving way to smaller ones lining the upper orbital margin. The small orbits are rounded, the antennar fossae obliquely ovate.

The marginal parts of the cervical and hepatic furrows are barely discernible. Weak depressions separate the urogastric from the mesobranchial lobes. The pentagonal cardiac region is tumid and separated by broad grooves from the branchial regions and bounded behind by a narrow, flattened area from the posterior margin.

With the exception of a narrow beaded strip bordering the anterolateral margins and the bottom of the furrows, the dorsal surface is densely covered with small granules of several diameters.

The pterygostomian region is subtriangular, granulate and projects beyond the anterolateral margin. There are a few small granules beneath the lateral spine.

On the ventral surface the sternites are covered with granules decreasing in size posteriorly and each pair of sternites is bordered by a row of fine granules. The 4th sternites are trapezoidal in outline and about twice as long as the 5th; the 5th and 6th pairs are subrectangular and the 7th and 8th are chordate; the outer posterior angle of the 4th–6th pairs is directed backwards. The very deep abdominal trough extends well beyond the 4th sternites and is rimmed by a row of coarse granules.

DISCUSSION. This species differs from *T. granulosus* by the sharp granulose lateral margin, the smooth band on the branchial regions parallel to the lateral margin, and the two or three rows of granules lining the frontal edge. We agree with Dr P. Müller (*in litt.* 6/12/1987) that *Nucia baripadensis* Bachmayer & Mohanti, 1973 is probably the same as *T. granulosus*.

Typilobus sp. Fig. 8

MATERIAL. An abraded internal mould In 46373 (Fig. 8). Locality NB 132, ?Lower Miocene Te_5–f, Simengaris Formation (Silimpopon horizon of Wenk, 1938). South-east part of Silimpopon area, Tawau, Cowie Harbour, Sabah.

REMARKS. In view of the characters so well preserved on the foregoing species, it would seem unwise to give a specific name to this rather poorly preserved specimen. The outline of the carapace, together with the low flattened profile and the thin lateral edge, are strongly reminiscent of *T. marginatus* sp. nov.

Section **THORACOTREMATA** Guinot, 1977

Superfamily **GRAPSOIDEA** Macleay, 1838

Family **GRAPSIDAE** Macleay, 1838

Genus ***PALAEOGRAPSUS*** Bittner, 1875

TYPE SPECIES. By subsequent designation of Glaessner, 1929: *Palaeograpsus inflatus* Bittner, 1875, from Upper Eocene of Vicentino, Italy.

RANGE. Middle Eocene to Pliocene.

Palaeograpsus bittneri sp. nov. Figs 66, 67

DIAGNOSIS. A *Palaeograpsus* with the lateral margins finely granulated and a larger granule bordering the epigastric lobe; the median part of the dorsal surface is weakly depressed.

NAME. For A. Bittner.

HOLOTYPE. In 61987 (Fig. 66), and paratypes In 61988 (Fig. 67), In 61989–93 from locality S.5538, Upper Miri Formation.

DESCRIPTION. The carapace is subquadrate, almost as broad as long. Short, rounded anterolateral margins lined with several small granules terminate at a weak notch more clearly seen in side view, where a shallow furrow extends back a little before curving to the front. Behind the notch is a larger granule followed by two or three smaller ones; the marginal edge then becomes rounded posteriorly. Long, shallow depressions for the 5th coxae lead by broadly rounded angles to the posterior margin, which is concave and about as wide as the front. The slightly produced front occupies half of the orbitofrontal margin and is almost straight on either side of a

Figs 46, 47 *Portunus woodwardi* sp. nov. From S.5548, Lower Miri Formation, × 2. Fig. 46, **holotype** (♂) In 61923. a, b, dorsal and ventral views. Fig. 47, paratype (♂) In 61924. a, b, dorsal and ventral views showing bopyriform swelling on the left branchial chamber.

Figs 48–53 *Podophthalmus fusiformis* sp. nov. from S.5550, Lower Miri Formation. Fig. 48, **holotype** In 62066, × 2. a, b, dorsal and anterior views. Fig. 49, dorsal view of paratype In 62067, × 3. Fig. 50, ventral view of paratype In 62068, × 3. Fig. 51, dorsal view of paratype In 62070, × 3. Fig. 52, dorsal view of paratype In 62071, × 3. Fig. 53, dorsal view of paratype In 62069, × 3.

Figs 54, 55 *Galene stipata* sp. nov. Fig. 54, **holotype** In 59014 from S.4965, Lower Miri Formation, × 1. a–d, dorsal, ventral, left lateral and anterior views. Fig. 55, anteroventral view to show right cheliped of paratype In 61958 from S.5548, Lower Miri Formation, × 2.

Figs 56a, b *Prepaeduma decapoda* gen. et sp. nov. **Holotype** In 61994 from S.5549, Lower Miri Formation, × 3. a, b, dorsal and ventral views. See also Figs 56c, d (p. 27).

NAME. Referring to the sharp lateral margin.

HOLOTYPE. In 62163 (Figs 7a–d) from locality NB 11541, Tungku Formation, Middle Miocene.

DESCRIPTION. The length of the transversely oval carapace is about four-fifths of the breadth measured immediately in front of the lateral spines; it is moderately arched transversely and longitudinally flatly arched behind a weak postfrontal depression. The anterolateral margins are convex with hardly any indentation at the cervical notch. The spine at the lateral angle is set a little behind the mid-carapace length. It is bluntly rounded and upturned, and anteriorly it tapers into a very thin edge lined with granules. At the cervical notch the ridge divides; the stronger, lower branch is interrupted by a large cluster of granules on the pterygostomian region and terminates in a small tubercle beneath the orbit, while the upper branch continues to the upper orbital margin. The posterolateral margins are nearly straight with a small, wart-like tubercle opposite the widest part of the cardiac region. A similar tubercle occurs at the posterior angle and the posterior margin is about as wide as the orbitofrontal margin. The orbitofrontal margin occupies a third of the carapace width and the sides of the barely projecting front are feebly inclined to a shallow median depression. The frontal edge is lined with two or three rows of fine granules, giving way to smaller ones lining the upper orbital margin. The small orbits are rounded, the antennar fossae obliquely ovate.

The marginal parts of the cervical and hepatic furrows are barely discernible. Weak depressions separate the urogastric from the mesobranchial lobes. The pentagonal cardiac region is tumid and separated by broad grooves from the branchial regions and bounded behind by a narrow, flattened area from the posterior margin.

With the exception of a narrow beaded strip bordering the anterolateral margins and the bottom of the furrows, the dorsal surface is densely covered with small granules of several diameters.

The pterygostomian region is subtriangular, granulate and projects beyond the anterolateral margin. There are a few small granules beneath the lateral spine.

On the ventral surface the sternites are covered with granules decreasing in size posteriorly and each pair of sternites is bordered by a row of fine granules. The 4th sternites are trapezoidal in outline and about twice as long as the 5th; the 5th and 6th pairs are subrectangular and the 7th and 8th are chordate; the outer posterior angle of the 4th–6th pairs is directed backwards. The very deep abdominal trough extends well beyond the 4th sternites and is rimmed by a row of coarse granules.

DISCUSSION. This species differs from *T. granulosus* by the sharp granulose lateral margin, the smooth band on the branchial regions parallel to the lateral margin, and the two or three rows of granules lining the frontal edge. We agree with Dr P. Müller (*in litt.* 6/12/1987) that *Nucia baripadensis* Bachmayer & Mohanti, 1973 is probably the same as *T. granulosus*.

Typilobus sp. Fig. 8

MATERIAL. An abraded internal mould In 46373 (Fig. 8). Locality NB 132, ?Lower Miocene Te_5–f, Simengaris Formation (Silimpopon horizon of Wenk, 1938). South-east part of Silimpopon area, Tawau, Cowie Harbour, Sabah.

REMARKS. In view of the characters so well preserved on the foregoing species, it would seem unwise to give a specific name to this rather poorly preserved specimen. The outline of the carapace, together with the low flattened profile and the thin lateral edge, are strongly reminiscent of *T. marginatus* sp. nov.

Section **THORACOTREMATA** Guinot, 1977

Superfamily **GRAPSOIDEA** Macleay, 1838

Family **GRAPSIDAE** Macleay, 1838

Genus ***PALAEOGRAPSUS*** Bittner, 1875

TYPE SPECIES. By subsequent designation of Glaessner, 1929: *Palaeograpsus inflatus* Bittner, 1875, from Upper Eocene of Vicentino, Italy.

RANGE. Middle Eocene to Pliocene.

Palaeograpsus bittneri sp. nov. Figs 66, 67

DIAGNOSIS. A *Palaeograpsus* with the lateral margins finely granulated and a larger granule bordering the epigastric lobe; the median part of the dorsal surface is weakly depressed.

NAME. For A. Bittner.

HOLOTYPE. In 61987 (Fig. 66), and paratypes In 61988 (Fig. 67), In 61989–93 from locality S.5538, Upper Miri Formation.

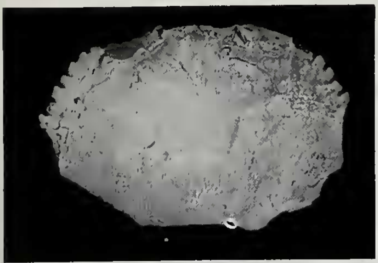
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Figs 46, 47 *Portunus woodwardi* sp. nov. From S.5548, Lower Miri Formation, × 2. Fig. 46, **holotype** (♂) In 61923. a, b, dorsal and ventral views. Fig. 47, paratype (♂) In 61924. a, b, dorsal and ventral views showing bopyriform swelling on the left branchial chamber.

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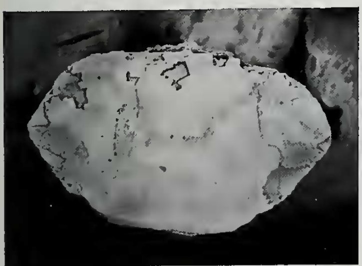
Figs 54, 55 *Galene stipata* sp. nov. Fig. 54, **holotype** In 59014 from S.4965, Lower Miri Formation, × 1. a–d, dorsal, ventral, left lateral and anterior views. Fig. 55, anteroventral view to show right cheliped of paratype In 61958 from S.5548, Lower Miri Formation, × 2.

Figs 56a, b *Prepaeduma decapoda* gen. et sp. nov. **Holotype** In 61994 from S.5549, Lower Miri Formation, × 3. a, b, dorsal and ventral views. See also Figs 56c, d (p. 27).


46a

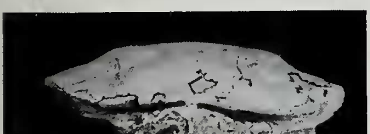

46b


47a


48a

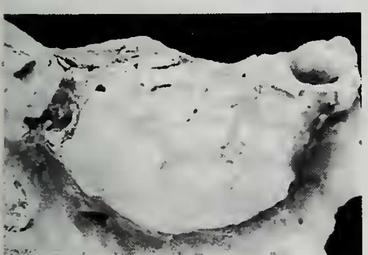

49


47b


48b


52


50


51

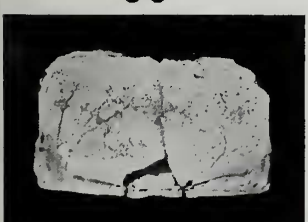

54a

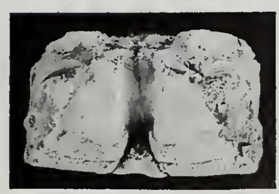

54b


53

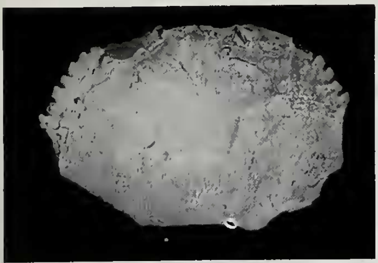

54c


54d


56a


56b


55


46a

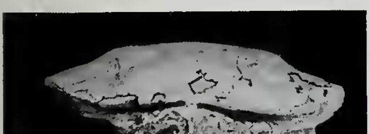

46b


47a


48a

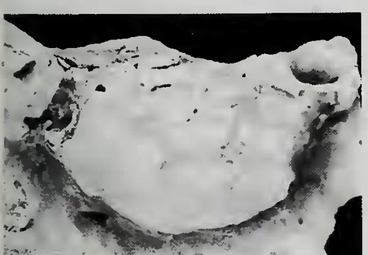

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47b


48b


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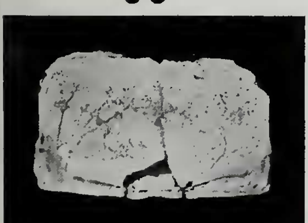

54a

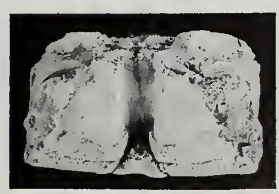

54b


53


54c


54d


56a


56b


55

slight median notch, emphasised above by weak epigastric lobes and bordered by a fine ridge continuing round the upper orbital margin. The upper orbital margin is weakly sinuous and terminates in an inconspicuous spine.

The postcervical furrow is strongest where it crosses the midline in a gentle curve; weakening at the outer angles of the mesogastric lobe, it extends forwards and outwards and becomes obsolete before reaching the margin. Very short epimeral adductor muscle scars separate the urocardiac from the branchiocardiac regions. Only the anterior process of the mesogastric lobe is clearly defined and internal moulds show a granule at the lower inner angle of the protogastric lobes. A depression across the base of the mesogastric and basal portions of the protogastric lobes appears deepened posteriorly by tumid mesobranchial lobes and a rounded ridge on the broadly pentagonal, fused cardiac region. Wide, deep furrows extend from the broadest part of the cardiac region parallel with the coxigeal incisions; anterior to these furrows, a shallower branchiocardiac furrow crosses the carapace margin and curves toward the front.

The chelipeds are of much the same length, although the left is the heavier; the manus equals about half the carapace width. The perieopods are long and slender; the merus of the 4th is similar in size to that of the 2nd and 3rd and a little longer than the 5th.

The telson of the male abdomen reaches as far as the 3rd/4th sternite border; the 4th sternites are triangular and the even-sized 5th/8th are chordate in outline.

Discussion. There is a remarkable similarity in the form of *Palaeograpsus bittneri* sp. nov. to *P. guerini* Via, 1959, from the Lutetian of Italy and Spain, to *P. depressus* Quayle & Collins, 1981 its possible derivative, and *P. bartonensis* Quayle & Collins, 1981, the last two from the Upper Eocene of the Hampshire Basin. In *P. bittneri*, however, the cervical furrow is reduced dorsally to a marginal notch; the postcervical is confined to the median part of the carapace and in these respects it is closer to the British species than to *P. guerini*. The front of *P. bittneri* is straighter and its outer angles sharper than in *P. guerini*, but probably not so far advanced as the similarly-shaped front of *P. depressus*.

Superfamily **PINNOTHEROIDEA** de Haan, 1833

Family **PINNOTHERIDAE** de Haan, 1833

Subfamily **PINNOTHERINAE** de Haan, 1833

Genus ***PINNIXA*** White, 1846

Type species. By original designation *Pinnotheres cylindricum* Say, 1818 [ICZN Opinion 85]; from Recent of Jekyll Island, Georgia, U.S.A.

Range. Oligocene to Recent.

Pinnixa aequipunctata sp. nov. Figs 58–61

Diagnosis. A *Pinnixa* with gastro-hepatic furrows more prominent than those dividing the branchial regions. There is a pit on either side of the midline and between them the cervical furrow is shallow: the dorsal surface of the branchial region is evenly pitted.

Name. Referring to the pitted branchial regions.

Holotype. In 61983 (Figs 58a, b), and paratypes In 61984 (Fig. 59), In 61985 (Fig. 60), In 61986 (Fig. 61). All from locality S.5539, Upper Miri Formation.

Description. Carapace with length a little more than half the breadth, moderately rounded longitudinally and nearly flat in transverse section. The antero- and posterolateral margins are well rounded, but leave the lateral margins shortly subparallel. The margin edges are acute and thinly beaded. Ovate orbits, occupying the outer thirds of the orbitofrontal margin, are slightly indented medially by a projection of the upper orbital margin and a short length of the ocular peduncle, seen on the type, is contracted coincidentally. The front is not well preserved. The furrow separating the hepatic from the gastric regions commences immediately behind the outer orbital angle, and is deeper than its posterior extension which partly divides the branchial region. The cervical furrow crosses the midline in a broad curve and is shallower between small pits on either side of the midline. The protogastric lobes are feebly separated anteriorly and only a very shallow furrow separates the confluent, almost circular urogastric and cardiac lobes from the branchial regions. Pits of even size crowd the branchial regions.

Discussion. So far, only a few fossil species of *Pinnixa* have been described; the earliest known, *P. eocenica* Rathbun, 1926 may be distinguished from *P. aequipunctata* in having a more rounded carapace outline, stronger branchial furrows and a narrower cardiac region. Rathbun (1932) described two Miocene species from California: of these *Pinnixa galliheri* differs from the Borneo species in having arcuate rather than straight lateral margins, while *P. montereyensis* is known by only one specimen showing its ventral surface. In the same paper Rathbun describes *Parapinnixa miocenica* (regarded by Via Boada, 1969, as *Pinnixa*) which also has angular lateral angles.

Pinnixa omega sp. nov. Fig. 62

Diagnosis. Carapace with deep grooves separating the mesogastric region from the protogastric region and the protogastric region from the hepatic lobes.

Figs 56c, d, 57 *Prepaeduma decapoda* gen. et sp. nov. Fig. 56c, d, **holotype** In 61994 from S.5549, Lower Miri Formation, × 3. c, d, left lateral and posteroventral views. See also Figs 56a, b (p. 25). Fig. 57, ventral view of paratype In 61996 from S.5550, Lower Miri Formation, × 3.

Figs 58–61 *Pinnixa aequipunctata* sp. nov. Fig. 58, **holotype** In 61983 from S.5539, Upper Miri Formation, × 3. a, b, dorsal and left lateral views of internal mould. Fig. 59, paratype In 61984 from S.5539, Upper Miri Formation, × 3. a, b, dorsal and anterior views of internal mould. Fig. 60, right oblique anterior view to show cheliped, paratype In 61985 from S.5539, Upper Miri Formation, × 5. Fig. 61, manus of right cheliped, paratype In 61986 from S.5539, Upper Miri Formation, × 10.

Fig. 62 *Pinnixa omega* sp. nov. **Holotype** In 61982 from S.5539, Upper Miri Formation, × 3. a, b, dorsal and anterior views.

Figs 63–65 *Xenophthalmus subitus* sp. nov. from S.5539, Upper Miri Formation, × 3. Fig. 63, **holotype** (♀) In 62097. a, b, dorsal and ventral views. Fig. 64, ventral view of abdomen, paratype (♂) In 62098. Fig. 65, ventral view of abdomen, paratype (♂) In 62099.

Figs 66, 67 *Palaeograpsus bittneri* sp. nov. from S.5538, Upper Miri Formation, × 3. Fig. 66, **holotype** In 61987, latex cast of external mould of dorsal. Fig. 67, paratype In 61988, latex cast of external mould of ventral.

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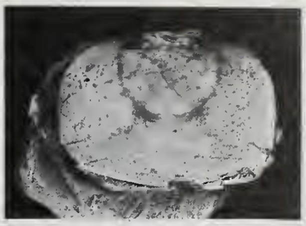
Fig. 62 *Pinnixa omega* sp. nov. **Holotype** In 61982 from S.5539, Upper Miri Formation, × 3. a, b, dorsal and anterior views.

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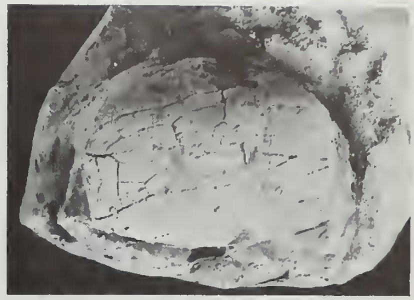
Figs 66, 67 *Palaeograpsus bittneri* sp. nov. from S.5538, Upper Miri Formation, × 3. Fig. 66, **holotype** In 61987, latex cast of external mould of dorsal. Fig. 67, paratype In 61988, latex cast of external mould of ventral.



56c



58a



59a



56d



58b



59b



57



62a



63a



63b



60



62b



64



65



61



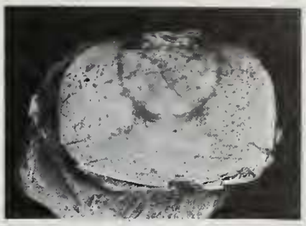
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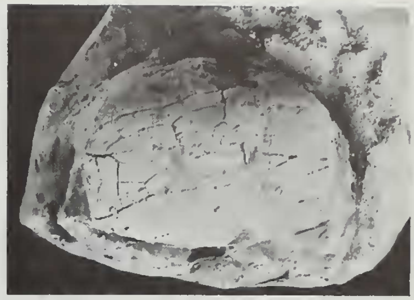
67



56c



58a



59a



56d



58b



59b



57



62a



60



63a



63b



62b



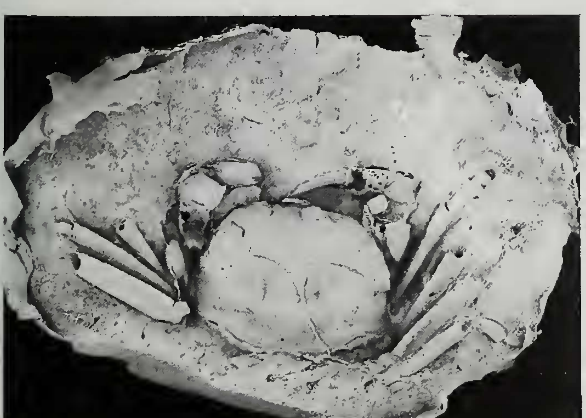
64



65



61



66



67

NAME. From the resemblance of the hepatic and gastric furrows to the Greek character.

HOLOTYPE. In 61982 (Figs 62a, b) from locality S.5539, Upper Miri Formation.

DESCRIPTION. The transversely subovate carapace is one-third broader than long, and nearly flat in both transverse and longitudinal sections. Small ovate orbits take up the outer fourths of the orbitofrontal margin, which occupies about a third of the carapace width. The upper orbital margin is slightly raised and the front (which is not well preserved) is emphasized above by minute frontal lobes set close to the tip of the anterior mesogastric process. The posterolateral margins are somewhat less rounded than the anterolateral margins, the posterior angle is acute and the wide posterior margin is weakly concave at its outer thirds and (possibly) convex medially; it is bounded by a fine rim. From wide, shallow marginal notches the cervical furrow extends broadly backwards and inwards. Becoming narrower, it curves sharply round the base of the hepatic region to unite with the gastro-hepatic and proto-mesogastric furrows before crossing the midline in a shallow curve; laterally it encloses a small tumid, triangular subhepatic region. From immediately behind the outer orbital angle the prominent gastro-hepatic furrow runs back for half its length, before turning angularly inwards; the proto-mesogastric furrow is only a little less wide. The hepatic regions are weakly tumid bordering the furrow, and the finely tapering anterior process of the isosceles-shaped mesogastric lobe extends to the front. The confluent urocardiac region is lingulate in outline.

DISCUSSION. The deeply incised gastric furrows and their characteristic outline immediately distinguishes *P. omega* from *P. aequipunctata* sp. nov., p. 26, and from all other species of *Pinnixa*. *Pinnixa* species are commonly commensal with annelid worms, living in their burrows and also in the burrows of worm-like holothurians.

Superfamily **HEXAPODOIDEA** Miers, 1886

Family **HEXAPODIDAE** Miers, 1886

Subfamily **HEXAPODINAE** Miers, 1886

Genus ***PREPAEDUMA*** nov.

TYPE SPECIES. *Prepaeduma decapoda* gen. et sp. nov. from the Pliocene of Borneo.

RANGE. Pliocene, Lower to Upper Miri Formation.

DIAGNOSIS. Hexapodid with fifth pair of pereiopods and eighth sternites fully exposed subdorsally. Female abdominal somites unfused; in the male the fourth and fifth abdominal somites are fused.

NAME. Precursor of *Paeduma*. Neuter.

DISCUSSION. Only one genus of hexapodid crab, *Paeduma* Rathbun, 1897 (= *Amorphopus* Bell, 1859 *non* Audinet-Serville, 1839) can be compared with *Prepaeduma*, because it is the only hexapodid genus bearing a fifth pereiopod, although Bell (1859) mentions in describing *Amorphopus cylindraceus* that the fifth pair of pereiopods were reduced to a mere rudiment. Bell further commented that on de Haan's figure he could detect a tubercle at the base of the fourth pereiopod which is probably a vestigial representative of the fifth pereiopod. Manning & Holthuis (1981: 174) transferred *Thaumastoplax orientalis* Rathbun, 1909, *T. chuensis* Rathbun, 1909, and an undescribed species from Japan identified by earlier workers as *T. orientalis*, from *Thaumastoplax* to *Paeduma*. Manning & Holthuis showed that all these species had the third with the fourth, and the fifth with the sixth, male abdominal segments fused, and that in all the abdomen extended forward to the posterior margin of the buccal cavity. *Thaumastoplax* is distinguished from *Paeduma* by having the third to fifth male abdominal segments fused, and the second ambulatory legs are by far the longest and strongest of the walking legs. We are unable to confirm the last character in *P. decapoda,* below, because unfortunately the legs are not preserved. *Thaumastoplax* and *Paeduma* are similar in lacking the oblique striae on the pterygostomian regions common in hexapodid genera.

As noted by Guinot (1979: 114) hexapodid crabs are generally commensal, living in the tubes of annelids and the cavities of hydrozoans. The body has become transversally elongated for ease of entry to these cavities, presumably associated with sideways walking. Guinot (1979: 115) noted that *Paeduma* seemed to conform to the twelfth [*recte*, eleventh] rule of Lankester (1904: 538–9), in which a tendency to atrophy will be seen generally in the front or rear of the tagma. In *Prepaeduma* we probably have an ancestral form in which all the segments and legs are present but in the male only abdominal somites four and five are fused.

Prepaeduma decapoda gen. et sp. nov. Figs 56, 57

DIAGNOSIS. As genus.

NAME. 'Ten-legged'.

HOLOTYPE. In 61994 (♂, Figs 56a–d), from Pliocene, Lower Miri Formation of locality S.5549. Paratypes In 61996 (♂, Fig. 57), In 61997–99 (11 specimens) from Pliocene, Lower Miri Formation of S.5550; paratypes In 62062–5 (6 specimens) from Pliocene, Upper Miri Formation of S.5539.

DESCRIPTION. Carapace length about three-quarters of the breadth; longitudinally very convex, particularly anteriorly, and nearly flat in transverse section. The anterolateral margins are narrowly rounded and the straight posterolateral margins lead by acute posterior angles into wide incisions abutting the 7th sternites. The posterior margin is straight and about as wide as the orbitofrontal margin which takes up about two-thirds of the carapace width. The front is not well preserved; it is rounded with the longitudinal curvature of the carapace and probably did not extend beyond the outer orbital spine. Anteriorly the margin edges are acute and finely ridged; the sides are inclined more or less at right angles to the dorsal surface and the subhepatic region is slightly tumid.

The regions are poorly defined and the cervical furrow is represented by little more than lines running towards the midline from a shallow pit at the head of short, moderately deep epimeral muscle scars. The broad, subtriangular cardiac region is clearly delineated from the branchial regions. Fine granules crowd the dorsal surface.

In the male the abdominal trough is rather narrow between the 6th sternites and broadens about midlength of the 5th pair. The 5th sternites are large, subtriangular with a broadly rounded basal angle and oblique basal edge; the median edge of the 6th pair protrudes slightly beyond the 5th and its basal

NAME. From the resemblance of the hepatic and gastric furrows to the Greek character.

HOLOTYPE. In 61982 (Figs 62a, b) from locality S.5539, Upper Miri Formation.

DESCRIPTION. The transversely subovate carapace is one-third broader than long, and nearly flat in both transverse and longitudinal sections. Small ovate orbits take up the outer fourths of the orbitofrontal margin, which occupies about a third of the carapace width. The upper orbital margin is slightly raised and the front (which is not well preserved) is emphasized above by minute frontal lobes set close to the tip of the anterior mesogastric process. The posterolateral margins are somewhat less rounded than the anterolateral margins, the posterior angle is acute and the wide posterior margin is weakly concave at its outer thirds and (possibly) convex medially; it is bounded by a fine rim. From wide, shallow marginal notches the cervical furrow extends broadly backwards and inwards. Becoming narrower, it curves sharply round the base of the hepatic region to unite with the gastro-hepatic and proto-mesogastric furrows before crossing the midline in a shallow curve; laterally it encloses a small tumid, triangular subhepatic region. From immediately behind the outer orbital angle the prominent gastro-hepatic furrow runs back for half its length, before turning angularly inwards; the proto-mesogastric furrow is only a little less wide. The hepatic regions are weakly tumid bordering the furrow, and the finely tapering anterior process of the isosceles-shaped mesogastric lobe extends to the front. The confluent urocardiac region is lingulate in outline.

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RANGE. Pliocene, Lower to Upper Miri Formation.

DIAGNOSIS. Hexapodid with fifth pair of pereiopods and eighth sternites fully exposed subdorsally. Female abdominal somites unfused; in the male the fourth and fifth abdominal somites are fused.

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DISCUSSION. Only one genus of hexapodid crab, *Paeduma* Rathbun, 1897 (= *Amorphopus* Bell, 1859 *non* Audinet-Serville, 1839) can be compared with *Prepaeduma*, because it is the only hexapodid genus bearing a fifth pereiopod, although Bell (1859) mentions in describing *Amorphopus cylindraceus* that the fifth pair of pereiopods were reduced to a mere rudiment. Bell further commented that on de Haan's figure he could detect a tubercle at the base of the fourth pereiopod which is probably a vestigial representative of the fifth pereiopod. Manning & Holthuis (1981: 174) transferred *Thaumastoplax orientalis* Rathbun, 1909, *T. chuensis* Rathbun, 1909, and an undescribed species from Japan identified by earlier workers as *T. orientalis*, from *Thaumastoplax* to *Paeduma*. Manning & Holthuis showed that all these species had the third with the fourth, and the fifth with the sixth, male abdominal segments fused, and that in all the abdomen extended forward to the posterior margin of the buccal cavity. *Thaumastoplax* is distinguished from *Paeduma* by having the third to fifth male abdominal segments fused, and the second ambulatory legs are by far the longest and strongest of the walking legs. We are unable to confirm the last character in *P. decapoda,* below, because unfortunately the legs are not preserved. *Thaumastoplax* and *Paeduma* are similar in lacking the oblique striae on the pterygostomian regions common in hexapodid genera.

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Prepaeduma decapoda gen. et sp. nov. Figs 56, 57

DIAGNOSIS. As genus.

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HOLOTYPE. In 61994 (♂, Figs 56a–d), from Pliocene, Lower Miri Formation of locality S.5549. Paratypes In 61996 (♂, Fig. 57), In 61997–99 (11 specimens) from Pliocene, Lower Miri Formation of S.5550; paratypes In 62062–5 (6 specimens) from Pliocene, Upper Miri Formation of S.5539.

DESCRIPTION. Carapace length about three-quarters of the breadth; longitudinally very convex, particularly anteriorly, and nearly flat in transverse section. The anterolateral margins are narrowly rounded and the straight posterolateral margins lead by acute posterior angles into wide incisions abutting the 7th sternites. The posterior margin is straight and about as wide as the orbitofrontal margin which takes up about two-thirds of the carapace width. The front is not well preserved; it is rounded with the longitudinal curvature of the carapace and probably did not extend beyond the outer orbital spine. Anteriorly the margin edges are acute and finely ridged; the sides are inclined more or less at right angles to the dorsal surface and the subhepatic region is slightly tumid.

The regions are poorly defined and the cervical furrow is represented by little more than lines running towards the midline from a shallow pit at the head of short, moderately deep epimeral muscle scars. The broad, subtriangular cardiac region is clearly delineated from the branchial regions. Fine granules crowd the dorsal surface.

In the male the abdominal trough is rather narrow between the 6th sternites and broadens about midlength of the 5th pair. The 5th sternites are large, subtriangular with a broadly rounded basal angle and oblique basal edge; the median edge of the 6th pair protrudes slightly beyond the 5th and its basal

edge is almost straight in contrast to the indented forward edge. The 7th pair is subrectangular in outline and is the longest.

In the female a fine suture with two pits separates the 4th sternites from the 5th pair which are trapezoidal, and their rounded basal angles protrude beyond the 6th. As in the male the 7th sternites are longest and all are inclined to the midline. The subovate female abdomen is broadest across the 3rd somite and the tip of the rather large subtriangular telson, rounded apically, extends the length of the 5th sternites. Only the small rectangular 3rd and 4th/5th somites of the male abdomen are preserved; the broken anterior margin of the '5th' is about half of the broadest part of the quadrate '4th'.

The male specimen (In 61996, Fig. 57) clearly shows the 5th pereiopod and 8th sternite, both of which are situated subdorsally. An 'appareil d'accrochage du type bouton-pression' (Guinot 1979: 120) is certainly present in the male, represented by a pit in the vertical wall of the abdominal trough on the 4th sternite situated just in front of the 4th/5th sternite boundary.

Discussion. *P. decapoda* is most similar to *Paeduma orientale* (Rathbun, 1909) but differs in the segments of the male abdomen. It is also comparable to *Hexapinus latipes* (de Haan, 1835), which has the third male abdominal segment fused to the fourth and fifth segments.

Subfamily **XENOPHTHALMINAE** Alcock, 1900

Genus ***XENOPHTHALMUS*** White, 1846

Type species. By monotypy *Xenophthalmus pinnotheroides* White, 1846, from the Recent of the Philippines.

Range. Pliocene to Recent.

Xenophthalmus subitus sp. nov. Figs 63–65

Diagnosis. Hepatic regions project anteriorly beyond the frontal region. Front with longitudinal groove which continues between the epigastric lobes. Discontinuous transverse ridge crosses the carapace at the level of the cardiac region.

Name. 'Sudden' or 'unexpected'.

Holotype. In 62097 (Figs 63a, b) and paratypes In 62098 (Fig. 64), In 62099 (Fig. 65), In 62100–19 from locality S.5539, Upper Miri Formation.

Description. The carapace is subovate, about one-fourth broader than long; moderately curved longitudinally, but downturned rather more steeply in front and nearly flat in transverse section. Short anterolateral margins are rounded continuously into the front and thinly ridged; the ridge is a little more accentuated at the outer orbital angles, but becomes obsolete behind the orbits. Anteriorly the sides are inclined at about right angles with a low ridge just above the pleural suture; they become rounded and splayed out posteriorly. Broad, rounded posterior angles lead by shallow incisions for the fifth coxae into a narrow posterior margin which is rather more steeply concave in the male. The very small orbits are obliquely ovate, in line with the longitudinal curvature of the carapace. The front is not produced, sulcate above with small terminal nodes followed by tumid, somewhat elongated epigastric lobes. A transverse, sinuous row of tubercles is formed by one median on the mesogastric lobe, two on each protogastric and one on each epibranchial lobe; behind these, smaller granules on the mesobranchial and one on either side of the median mesogastric form a second, almost parallel row. Another granule occurs just above the coxigeal incision. Curving across the metabranchial lobes a sharp ridge is interrrupted by grooves delimiting the broadly pentagonal cardiac region and continues across its broadest part.

The broadly ovate female abdomen covers the entire ventral surface. The 6th somite is fractionally larger than the 3rd–5th somites, and at the junction of each somite there is a pit in the trough on either side of the raised median portion; on the 3rd somite is a low transverse ridge. The male abdomen is about a third the width of that of the female and parallel-sided.

Discussion. The backward direction of the orbit suggests this species should be assigned to *Xenophthalmus*, but other characters on the carapace, especially the discontinuous transverse ridge level with the cardiac region, invites comparison with *Neoxenophthalmus obscurus* (Henderson, 1893) in which the ridge separates a punctate area from the smooth posterior region. The holotype (In 62097) has the peduncles of the eyes deformed, giving a misleading impression that the orbits are inclined at an oblique angle to the midline (Fig. 63a). The Brunei species has all the regions more strongly expressed than in *Xenophthalmus pinnotheroides* White, 1846, and lacks the ridge from the posterior margin crossing the metabranchial and joining the cardiac transverse ridge.

This group of hexapodids is probably commensal with annelids in relatively shallow water in the 5–30m range and on a muddy bottom.

Superfamily **OCYPODOIDEA** Rafinesque, 1815

Family **OCYPODIDAE** Rafinesque, 1815

Subfamily **MACROPHTHALMINAE** Dana, 1852

Genus ***MACROPHTHALMUS*** Latreille, *in* Desmarest 1823

Type species. By subsequent designation of H. Milne Edwards, May, 1841: *Gonoplax transversus* Latreille, 1817; from Recent of the Indian Ocean.

Range. Miocene to Recent.

Subgenus ***MAREOTIS*** Barnes, 1967

Type species. By original designation *Macrophthalmus japonicus* de Haan, 1835; from Recent of the Indo-Pacific region.

Range. Pliocene to Recent.

Macrophthalmus (Mareotis) wilfordi sp. nov. Figs 68–72

1961 *Macrophthalmus latreilli* (Desmarest): Wilford: 102; pl. 39.

Diagnosis. The carapace is widest between the tips of the outer orbital spines; without transverse lines of granules on the dorsal surface; the fixed finger of the cheliped is depressed.

Name. For G.E. Wilford.

Holotype. In 59000 (Figs 68a, b). Paratypes In 59001–4,

edge is almost straight in contrast to the indented forward edge. The 7th pair is subrectangular in outline and is the longest.

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Macrophthalmus (Mareotis) wilfordi sp. nov. Figs 68–72

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DIAGNOSIS. The carapace is widest between the tips of the outer orbital spines; without transverse lines of granules on the dorsal surface; the fixed finger of the cheliped is depressed.

NAME. For G.E. Wilford.

HOLOTYPE. In 59000 (Figs 68a, b). Paratypes In 59001–4,



68a



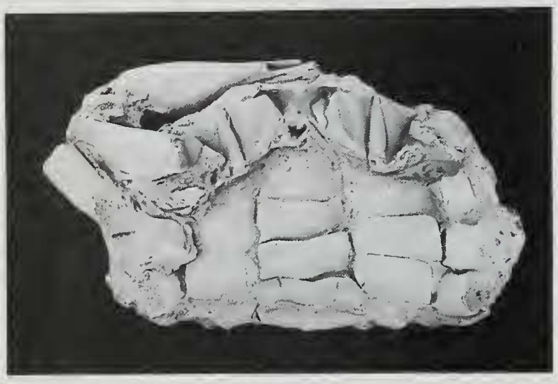
69a



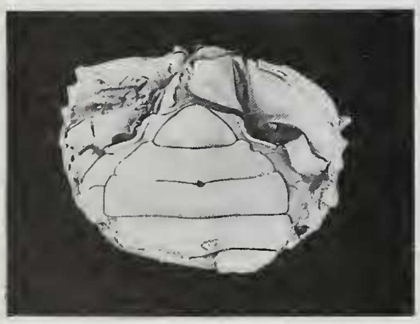
68b



69c



69b



70



71



72

Figs 68–72 *Macrophthalmus (Mareotis) wilfordi* sp. nov. from S.4918, ?late Middle Pleistocene. Fig. 68, **holotype** In 59000, × 1. a, b, dorsal and anterior views. Fig. 69, paratype In 62120. a, anterolateral angle and incomplete cheliped, × 3. b, ventral view, × 1.5. c, epistome, × 3. Fig. 70, ventral view of abdomen, paratype (♀) In 59005, × 1.5. Fig. 71, ventral view of abdomen, paratype (♂) In 59008, × 1. Fig. 72, propodus, paratype In 61810, × 1.



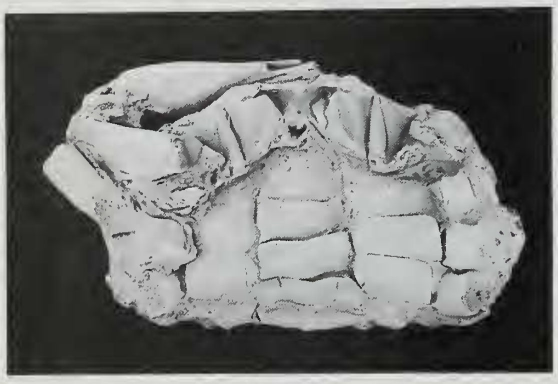
68a



68b



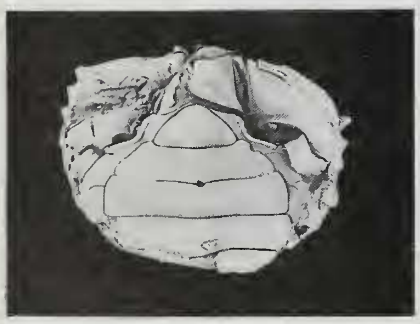
69a



69b



69c



70



71



72

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Table 2 Stratigraphical distribution of fossil crab species from the Neogene of Borneo.

	Lower Miocene	Middle Miocene	Upper Miocene	Lower Miri Fm	Upper Miri Fm	Seria Fm	Middle Pleistocene
Raninoides sp.	–	–	–	–	×	–	–
Dorippe frascone (Herbst) *tuberculata* subsp. nov.	–	–	–	×	–	–	–
Calappa sexaspinosa sp. nov.	–	–	–	×	–	–	–
Podophthalmus fusiformis sp. nov.	–	–	–	×	–	–	–
Charybdis feriata (Linn.) *bruneiensis* subsp. nov.	–	–	–	–	–	–	×
Portunus obvallatus sp. nov.	–	–	–	×	×	–	–
Portunus woodwardi sp. nov.	–	–	–	×	×	–	–
Galene stipata sp. nov.	–	–	–	×	×	×	–
Parthenope (Rhinolambrus) sublitoralis sp. nov.	–	–	–	×	–	–	–
Ampliura simplex gen. et sp. nov.	–	–	–	–	–	×	–
Drachiella guinotae sp. nov.	–	–	–	×	–	–	–
Iphiculus granulatus sp. nov.	–	–	–	–	–	×	–
Iphiculus miriensis sp. nov.	–	–	–	×	×	–	–
Iphiculus sexspinosus sp. nov.	–	–	–	–	×	×	–
Leucosia longiangulata sp. nov.	–	–	–	×	–	–	–
Leucosia serenei sp. nov.	–	–	–	×	×	–	–
Leucosia tutongensis sp. nov.	–	–	–	×	×	–	–
Myra brevisulcata sp. nov.	–	–	–	×	–	–	–
Myra subcarinata sp. nov.	–	–	–	×	×	–	–
Myra trispinosa sp. nov.	–	–	–	×	×	–	–
Nucia borneoensis sp. nov.	–	–	–	×	–	–	–
Nucia calculoides sp. nov.	–	–	–	×	–	–	–
Nucia coxi sp. nov.	×	–	–	–	–	–	–
Nucilobus symmetricus gen. et sp. nov.	–	–	–	×	–	–	–
Pariphiculus gselli Beets *beetsi* subsp. nov.	–	–	–	×	–	–	–
Pariphiculus papillosus sp. nov.	–	–	–	×	–	–	–
Pariphiculus verrucosus sp. nov.	–	–	–	×	–	–	–
Philyra granulosa sp. nov.	–	–	–	×	×	–	–
Typilobus marginatus sp. nov.	–	×	–	–	–	–	–
Typilobus sp.	×	–	–	–	–	–	–
Palaeograpsus bittneri sp. nov.	–	–	–	–	×	–	–
Pinnixa aequipunctata sp. nov.	–	–	–	–	×	–	–
Pinnixa omega sp. nov.	–	–	–	–	×	–	–
Prepaeduma decapoda gen. et sp. nov.	–	–	–	×	×	–	–
Xenophthalmus subitus sp. nov.	–	–	–	–	×	–	–
Macrophthalmus (Mareotis) wilfordi sp. nov.	–	–	–	–	–	–	×

In 59005 (Fig. 70), In 59006–7, In 59008 (Fig. 71), In 59009–11 (about 50 specimens), In 61810 (Fig. 72), In 62120 (Figs 69a–c). All from locality S.4918, ? late Middle Pleistocene.

Description. The carapace is subquadrate in outline, widest between the tips of the outer orbital spines and with the regions distinctly defined by furrows. The moderately bilobed front is narrow, deflexed and constricted between the bases of the ocular peduncles; the front edge is smooth but the sides are finely granulate; there is a deep, narrow median furrow and a few surface granules. The upper orbital border is curved and slopes slightly backwards; the margin is lined with small, rounded granules; the lower orbital margin is studded along its entire length with longer, tubercular granules. The outer orbital spine is large, rectangular with granulated margins; it is directed outwards and slightly forwards and is separated from the 2nd lateral spine by a broad U-shaped notch. The 2nd lateral spine is somewhat weaker than the former and does not project beyond it, its anterior margin is convex and both that and the posterior one are weakly granulate; a shallow notch separates it from the small, triangular 3rd lateral spine.

With the exception of a narrow frontal strip and a few small central areas the dorsal surface is covered with coarse granules. On each metabranchial region two longitudinal rows of granules extend subparallel to the lateral margin; the inner row is 'broken' and becomes sigmoidal centrally. The lateral margins are subparallel and lined with granules.

The sides of the 4th and 5th somites of the male abdomen are nearly straight and parallel, while the sides of the 6th are slightly convex and taper a little distally.

The chelipeds associated with the carapaces are incomplete, and of those attributed to *M. wilfordi* none has a ridge on the outer margin of the palm, the upper part of the outer margin is granulate especially proximally, and the lower margin is smooth. The fixed finger is deflexed and one left-hand example has a large crenulated tooth proximally on the cutting edge, and the lower margin is granulate with the granules decreasing in size distally.

Discussion. In having a narrow front with a well-developed ocular constriction, longitudinal granulate rows on the metabranchial lobes, a deflexed finger and, in the male, an abdomen with sides almost parallel, it would appear that the new species has already diverged considerably from the hypothetical ancestral form as envisaged by Barnes (1967: 250).

Macrophthalmus wilfordi has all the general characters essential to the subgenus *Mareotis* which one can reasonably expect to find preserved among fossil specimens. The occur-

Table 2 Stratigraphical distribution of fossil crab species from the Neogene of Borneo.

	Lower Miocene	Middle Miocene	Upper Miocene	Lower Miri Fm	Upper Miri Fm	Seria Fm	Middle Pleistocene
Raninoides sp.	–	–	–	–	×	–	–
Dorippe frascone (Herbst) *tuberculata* subsp. nov.	–	–	–	×	–	–	–
Calappa sexaspinosa sp. nov.	–	–	–	×	–	–	–
Podophthalmus fusiformis sp. nov.	–	–	–	×	–	–	–
Charybdis feriata (Linn.) *bruneiensis* subsp. nov.	–	–	–	–	–	–	×
Portunus obvallatus sp. nov.	–	–	–	×	×	–	–
Portunus woodwardi sp. nov.	–	–	–	×	×	–	–
Galene stipata sp. nov.	–	–	–	×	×	×	–
Parthenope (Rhinolambrus) sublitoralis sp. nov.	–	–	–	×	–	–	–
Ampliura simplex gen. et sp. nov.	–	–	–	–	–	×	–
Drachiella guinotae sp. nov.	–	–	–	×	–	–	–
Iphiculus granulatus sp. nov.	–	–	–	–	–	×	–
Iphiculus miriensis sp. nov.	–	–	–	×	×	–	–
Iphiculus sexspinosus sp. nov.	–	–	–	–	×	×	–
Leucosia longiangulata sp. nov.	–	–	–	×	–	–	–
Leucosia serenei sp. nov.	–	–	–	×	×	–	–
Leucosia tutongensis sp. nov.	–	–	–	×	×	–	–
Myra brevisulcata sp. nov.	–	–	–	×	–	–	–
Myra subcarinata sp. nov.	–	–	–	×	×	–	–
Myra trispinosa sp. nov.	–	–	–	×	×	–	–
Nucia borneoensis sp. nov.	–	–	–	×	–	–	–
Nucia calculoides sp. nov.	–	–	–	×	–	–	–
Nucia coxi sp. nov.	×	–	–	–	–	–	–
Nucilobus symmetricus gen. et sp. nov.	–	–	–	×	–	–	–
Pariphiculus gselli Beets *beetsi* subsp. nov.	–	–	–	×	–	–	–
Pariphiculus papillosus sp. nov.	–	–	–	×	–	–	–
Pariphiculus verrucosus sp. nov.	–	–	–	×	–	–	–
Philyra granulosa sp. nov.	–	–	–	×	×	–	–
Typilobus marginatus sp. nov.	–	×	–	–	–	–	–
Typilobus sp.	×	–	–	–	–	–	–
Palaeograpsus bittneri sp. nov.	–	–	–	–	×	–	–
Pinnixa aequipunctata sp. nov.	–	–	–	–	×	–	–
Pinnixa omega sp. nov.	–	–	–	–	×	–	–
Prepaeduma decapoda gen. et sp. nov.	–	–	–	×	×	–	–
Xenophthalmus subitus sp. nov.	–	–	–	–	×	–	–
Macrophthalmus (Mareotis) wilfordi sp. nov.	–	–	–	–	–	–	×

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rence of the greatest carapace width across the tips of the outer orbital spines instead of the 2nd anterolateral spines (common to the extant species of *Mareotis*) cannot be considered sufficient grounds to exclude it from that subgenus.

Of the nine Recent species placed by Barnes (1967, 1970) in *Mareotis*, *M. japonicus* de Haan compares favourably with and could well be descended from *M. wilfordi*. Apart from the position of the greatest carapace width, the former species may be distinguished by the upper and lower orbital margins being studded with similar-sized granules, by the absence of granules lining the frontal margin, and the presence of a transverse row of granules on the metabranchial lobes. According to Barnes (1967: 226) the inner longitudinal row of granules on the metabranchial lobes on Japanese forms of the Recent species is 'broken', as in *M. wilfordi*, while in Australian and North Chinese forms (Barnes 1970; 228) it is entire.

A superficial resemblance exists between *M. wilfordi* and *M.* (*Euplax*) *latreillei* (Desmarest, 1817), but the latter may be distinguished by the straight orbitofrontal margin, transverse rows of granules on the metabranchial lobes and a straight, undeflexed fixed finger.

Note. Barnes (1966), in revising the genus *Euplax* H. Milne Edwards, 1852 (type species *E. leptophthalmus* Milne Edwards, 1852, by subsequent designation of Barnes, 1966: 370) noted that *E. leptophthalmus* belonged to *Macrophthalmus* of the *M. latreillei* group. Later, Barnes (1967) erected a series of subgenera for the genus *Macrophthalmus*, including *M.* (*Venitus*) with type species by original designation *M. latreillei* (Desmarest, 1817). Thus it can be seen that *Euplax* is in fact a senior subjective synonym of *Venitus*. Further *Cyphoplax* Haime, 1855 (type species *Goneplax impressa* Desmarest, 1817 by monotypy, = *M. latreillei* (Barnes 1977: 280)) is also a senior subjective synonym of *Venitus*, but a junior subjective synonym of *Euplax*.

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